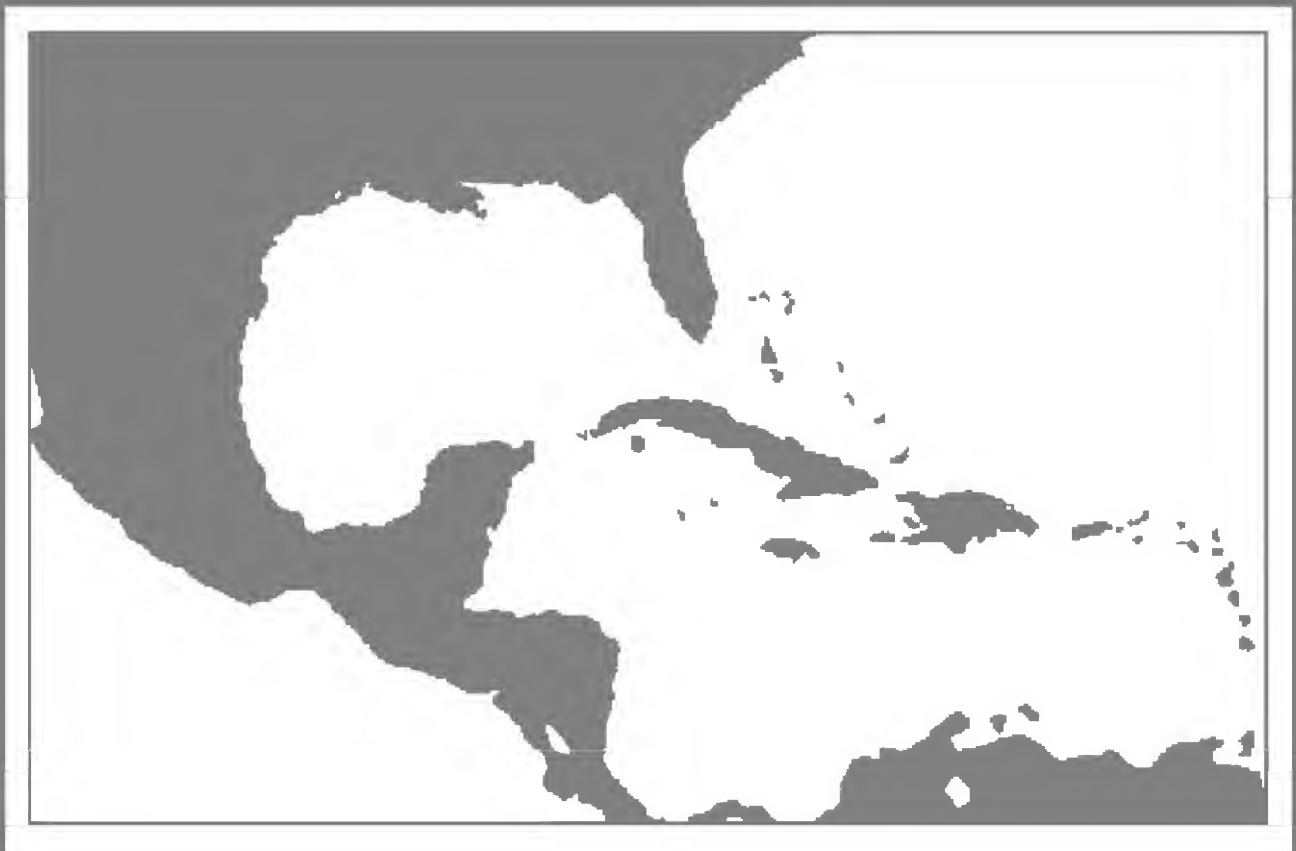


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HABITAT USE BY JUVENILE GAG, *MYCTEROPERCA MICROLEPIS* (PISCES: SERRANIDAE), IN SUBTROPICAL CHARLOTTE HARBOR, FLORIDA (USA)

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ABSTRACT Estuaries play a key role in the juvenile stage of gag (*Mycteroperca microlepis*). The use of estuarine habitats by juvenile gag has been examined in temperate estuaries, which are at the northern limits of the range of this species, but the importance of subtropical estuaries during the early life history of this species has not been studied extensively. Gag were collected in subtropical Charlotte Harbor, Florida, during routine monthly sampling from January 1996 to December 2002. Juvenile gag were collected using a 21.3-m seine, a 183-m haul seine, and a 183-m purse seine. A total of 738 individuals ranging from 30 to 489 mm standard length (SL) were collected in 4,480 samples. Most gag (96%) were probably young-of-the-year (< 288 mm SL). The majority of juveniles were collected in polyhaline Gasparilla and Pine Island sounds from April to December, with a few larger individuals captured year-round. The observed period of gag settlement was similar to that reported in other subtropical and temperate estuaries, but gag in Charlotte Harbor remained in the estuary longer and egressed at a larger size than did gag in other estuaries. Relative abundance of juvenile gag within Charlotte Harbor was greatest on shallow seagrass shoals but was also high along fringing mangrove shorelines, which is a habitat not previously reported for gag.

INTRODUCTION

Estuaries play a key role in the juvenile stage of gag (*Mycteroperca microlepis*) (Keener et al. 1988). The species ranges from New York to Brazil, including the entire Gulf of Mexico (GOM), and juveniles have been reported to occur in temperate and subtropical estuaries from Virginia to the northeastern GOM (Hoesle et al. 1961, Hood and Schlieder 1992, Koenig and Coleman 1998). This economically important serranid spawns in large aggregations, such as those found at traditional West Florida Shelf sites in the GOM, primarily during February and March (Hood and Schlieder 1992, Collins et al. 1998). The planktonic larvae move into estuaries and settle out at about 15 mm standard length (SL) in the first available habitat, such as polyhaline seagrass beds and oyster shell habitats near inlets and mouths of tidal creeks (Ross and Moser 1995, Mullaney and Gale 1996). As juvenile gag grow rapidly during their estuarine residence, they may also use manmade habitats like seawalls and jetties (Hastings 1979, Bullock and Smith 1991).

Latitudinal differences in climate appear to affect the duration of estuarine residence and size attained by juvenile gag before they disperse to non-estuarine habitats (Ross and Moser 1995). Juveniles are usually found in North Carolina estuaries from April to September and in estuaries along the northeastern GOM from April to October (Ross and Moser 1995, Koenig and Coleman 1998). The first cold front of fall is thought to trigger their egress to deeper ocean water (e.g., Ross and Moser

1995). In temperate estuaries such as Bogue Sound, North Carolina, maximum reported size does not exceed 200 mm SL (Ross and Moser 1995), but in subtropical estuaries such as Tampa Bay, Florida, gag can reach 360 mm SL (Hood and Schlieder 1992).

Habitat use by juvenile gag has been examined in temperate estuaries, which are at the northern limits of the range of this species; however, the importance of subtropical estuaries during the early life history of this species has not been studied extensively. Despite the effects of increasing urbanization and the resultant demands for freshwater resources, Charlotte Harbor, a large subtropical estuary in southwestern Florida, supports many suitable habitats for juvenile gag (e.g., seagrass beds, oyster shell habitats). Although juveniles have been collected from seagrass beds within the estuary (Wang and Raney 1971, Hanson et al. 2004, Fitzhugh et al. 2005), questions regarding aspects of habitat use, especially use of tropical climate habitats like mangroves, have not been examined. Thus, the objective of this study was to use an estuary-wide dataset from a long-term fisheries-independent monitoring program in Charlotte Harbor to examine distribution, seasonality, habitat use, and relative abundance of juvenile gag in a subtropical estuary.

MATERIALS AND METHODS

Study location

Charlotte Harbor, located on the southwestern coast of Florida, is one of the largest estuaries in Florida and

is separated from the GOM by a series of barrier islands. Two large inlets, Boca Grande Pass and San Carlos Pass, and four smaller inlets allow tidal water exchange. The modal depth of the estuary is 3–4 m, and the deepest point is 15.5 m in Boca Grande Pass (Huang 1966). The climate is subtropical, with infrequent freezes and distinct wet and dry seasons. Mean annual rainfall is 127 cm, 60% of which falls between June and September (Taylor 1974), whereas mean water temperature is 25°C, ranging from 12°C to 36°C, and mean salinity is 29 psu, ranging from 5 psu to 40 psu (Poulakis et al. 2003, present study).

Charlotte Harbor supports a variety of habitats that are used by at least 255 species of fish (Poulakis et al. 2004). The 2 predominant habitats for fishes are seagrass flats and fringing mangroves. Red mangrove (*Rhizophora mangle*), white mangrove (*Laguncularia racemosa*), and black mangrove (*Avicennia germinans*) are the 3 species found in Charlotte Harbor, but red mangroves dominate along the shoreline (143 km²; Poulakis et al. 2003). Turtle grass (*Thalassia testudinum*), shoal grass (*Halodule wrightii*), and manatee grass (*Syringodium filiforme*) are the most common seagrass species in the estuary (262 km²; Sargent et al. 1995). Other habitats found in Charlotte Harbor include oyster bars, sandy shoals (areas away from shore that are ≤ 0.5 m deep at mean low tide), seawalls, and bridge pilings.

Sample collection

Fish abundance and habitat data collected throughout Charlotte Harbor by the Florida Fish and Wildlife Conservation Commission (FWC), Fish and Wildlife Research Institute's Fisheries-Independent Monitoring program from January 1996 to December 2002 were analyzed for this study. Monthly stratified-random sampling was conducted during the day by using 3 different seines. Between 17 and 32 samples were completed each month for each gear, with effort distributed equally throughout the study area. The estuary was divided into 1 x 1 nautical-mile cartographic grids (1 nm²), and grids with appropriate water depths for each seine (≤ 1.5 m for 21.3 m seine, ≤ 2.5 m for 183-m haul seine, ≤ 3.3 m for 183-m purse seine) were selected as the sampling universe. Using a 10 x 10 cell overlay, each cartographic grid was subdivided into 100 microgrids (0.1 x 0.1 nm), which represented the potential sample sites that were randomly selected without replacement each month.

Samples were stratified by habitat type depending on gear. The 21.3-m center-bag seine (21.3 m x 1.8 m, 3.2-mm stretch mesh) was pulled along shorelines and on shoals away from shore (Poulakis et al. 2003). Samples collected with the 183-m center-bag haul seine (183 m x 3 m, 37.5-

mm stretch mesh) were stratified based on the presence or absence of overhanging shoreline vegetation (e.g., fringing mangroves). This seine was deployed by boat, in a rectangular shape (40 m x 103 m), along shorelines and on offshore flats inside the estuary and retrieved by hand (Kupschus and Tremain 2001). The 183-m terminal-bag purse seine (183 m x 5.2 m, 50-mm stretch mesh) was set at least 40 m from the shoreline and was retrieved with the aid of a motorized hydraulic system (Wessel and Winner 2003). All fishes were identified to the lowest possible taxon and enumerated. Up to 40 fishes were measured to the nearest millimeter SL, and all juvenile gag were released alive in the field. The bottom type, seagrass species, shoreline vegetation species, and coverage (%) of each sample were qualitatively measured. Salinity (psu), dissolved oxygen (mg l⁻¹), and water temperature (°C) were recorded with a hand-held data sonde. A vertical profile of these parameters was taken at the surface (0.2 m below surface) and at each whole meter increment until reaching the bottom (0.2 m above bottom).

Data analysis

The locations of captured juvenile gag were plotted by gear type to examine distribution throughout the estuary. Three size-classes were plotted separately (≤ 100 mm, 101 ≤ 250 mm, and ≥ 251 mm) to explore possible differences in ontogenetic distribution within the estuary. To examine seasonality, length-frequency data were divided into 10-mm size-classes and pooled by month and year for each gear to examine month of settlement, growth and relative abundance during estuarine residency, month of egress from estuary, and gear selectivity.

The gear type and areas within Charlotte Harbor where gag were most abundant were analyzed further by analysis of covariance (ANCOVA), which was performed by using a general linear modeling (GLM) approach, to investigate the influence of water temperature, salinity, water depth, overall seagrass coverage, bottom type, shoreline type, year, month, and geographic location on the gear-specific relative abundance of gag (PROC GLM; SAS Institute 1988). The relative abundance of gag was $\ln(x + 1)$ transformed before analysis.

Water temperature, salinity, water depth, and overall seagrass percent coverage were the covariates (continuous variables) and were $\ln(x + 1)$ transformed to stabilize the variance in the data before analysis. The value of each abiotic covariate used in the model was the mean of all readings taken at each sample location. We tested for parallelism in the model by plotting each covariate against gag relative abundance to ensure similar slopes.

Bottom type (i.e., sand, mud, oyster), shoreline vs. shoal, year, month, and geographic location were the class variables (categorical variables) in the model. Samples were excluded from all habitat analyses when the overall seagrass coverage could not be estimated due to poor water clarity or water depth (3.5% of all samples). The geographic location variable included data west of the dotted line in Figure 1 and was defined as areas north of Boca Grande Pass (Gasparilla Sound) and south of Boca Grande Pass (Pine Island Sound). For the shoreline vs. shoal class variable, "shoreline" was defined as the habitat at the land-water interface (i.e., mangroves, beach, seawall), and "shoal" was defined as areas that were ≤ 0.5 m deep at mean low tide and were at least 5 m from the shoreline (i.e., oyster bar, sand bar).

We constructed a full model that included all class variables and covariates and then simplified it using a stepwise elimination procedure. The variables with the highest P values were removed from the model one at a time until all remaining variables were significant at $\alpha = 0.01$. The significance level of 0.01 was used to minimize the possibility of Type I error. We report only significant class variables and covariates in the results. Tukey's Studentized Range (HSD) test was used post-hoc to determine where differences occurred in each significant variable (Zar 1999).

RESULTS

A total of 738 juvenile gag ranging from 30 to 489 mm SL were collected in 4,480 samples (Table 1). Most gag (96%) were probably young-of-the-year (< 288 mm SL), based on data presented in Hood and Schlieder (1992). Most juveniles were collected in the 183-m haul seine ($n = 615$) and ranged from 88 to 440 mm SL (mean = 183 mm). The purse seine collected individuals ($n = 83$) ranging from 50 to 489 mm SL (mean = 204 mm), and the 21.3-m seine collected juveniles ($n = 40$) ranging from 30 to 204 mm SL (mean = 138 mm).

Although samples were taken throughout the estuary (note locations of zero catches in Figure 1), gag were collected principally (95%) in polyhaline Gasparilla and Pine Island sounds (Table 1, Figure 1). Distribution plots of different size classes of gag showed that their distribution did not change as they grew, regardless of size or month, so all gag are included in Figure 1. The salinity (mean $\pm s_x$) where gag were captured was relatively consistent (31.0 ± 0.4 psu, range = 13–40 psu).

Gag were collected mainly from April to December, but some individuals were captured in all months (Figure 2). Juvenile gag ranging from 30 to 88 mm SL were cap-

tured in April and May. The cohorts grew and accumulated in numbers during June and July, with the highest number of gag collected in September. Although most individuals were captured from May to December in the haul seine, increasing numbers of individuals were collected in the purse seine in October and November as overall numbers declined in the estuary. Some of the previous years' cohorts (> 288 mm SL) were collected year-round (Figure 2). The mean water temperature ($\pm s_x$) where gag were captured was $27.7 \pm 0.3^\circ\text{C}$ (range = 14.5 – 33.5°C).

Because 78% of all gag were captured in the haul seine from May to December in Gasparilla and Pine Island sounds (Table 1), we used only these data in the general linear model to examine specific habitat use in areas and times when gag were most abundant. The variables that significantly affected gag abundance were geographic location (Pine Island Sound vs. Gasparilla Sound), year, month, water depth, shoreline vs. shoal, and overall seagrass percent cover (ANCOVA; $r^2 = 0.25$; Table 2). In Gasparilla and Pine Island sounds, the annual relative abundance of juvenile gag in 2002 was at least 2.7 gag per haul greater than in other years (Tukey's Studentized Range test; $P < 0.05$) (Figure 3). Gag abundances in Gasparilla and Pine Island sounds were significantly lower in May and December than in June through November (Tukey's Studentized Range test; $P < 0.05$). Gag were significantly more abundant in Gasparilla Sound than they were in Pine Island Sound (Tukey's Studentized Range test; $P < 0.05$). Mean water temperature and salinity varied little during May to December in both Gasparilla and Pine Island sounds and did not contribute to the model.

In Gasparilla and Pine Island sounds, juvenile gag were collected principally in habitats that contained $\geq 50\%$ overall seagrass coverage (Figure 4). Relative abundance on shoals was 2.9 fish per haul greater than near mangrove and beach shorelines (Tukey's Studentized Range test; $P < 0.05$). Only 8 of the shoal samples were on oyster bars (19 gag collected); the other 30 samples were on shoals that had $\geq 50\%$ overall seagrass coverage (133 gag collected). The majority of sample sites ($n = 280$) were along mangrove shorelines that had $\geq 50\%$ overall seagrass coverage, and that is where most of the juvenile gag ($n = 226$) were collected. The catch-per-unit-effort increased from 0.3 to 1.4 gag per haul when the bag depth was greater than one meter.

DISCUSSION

Juvenile gag are typically concentrated in polyhaline areas close to passes, and these areas apparently represent the first suitable environments that presettlement

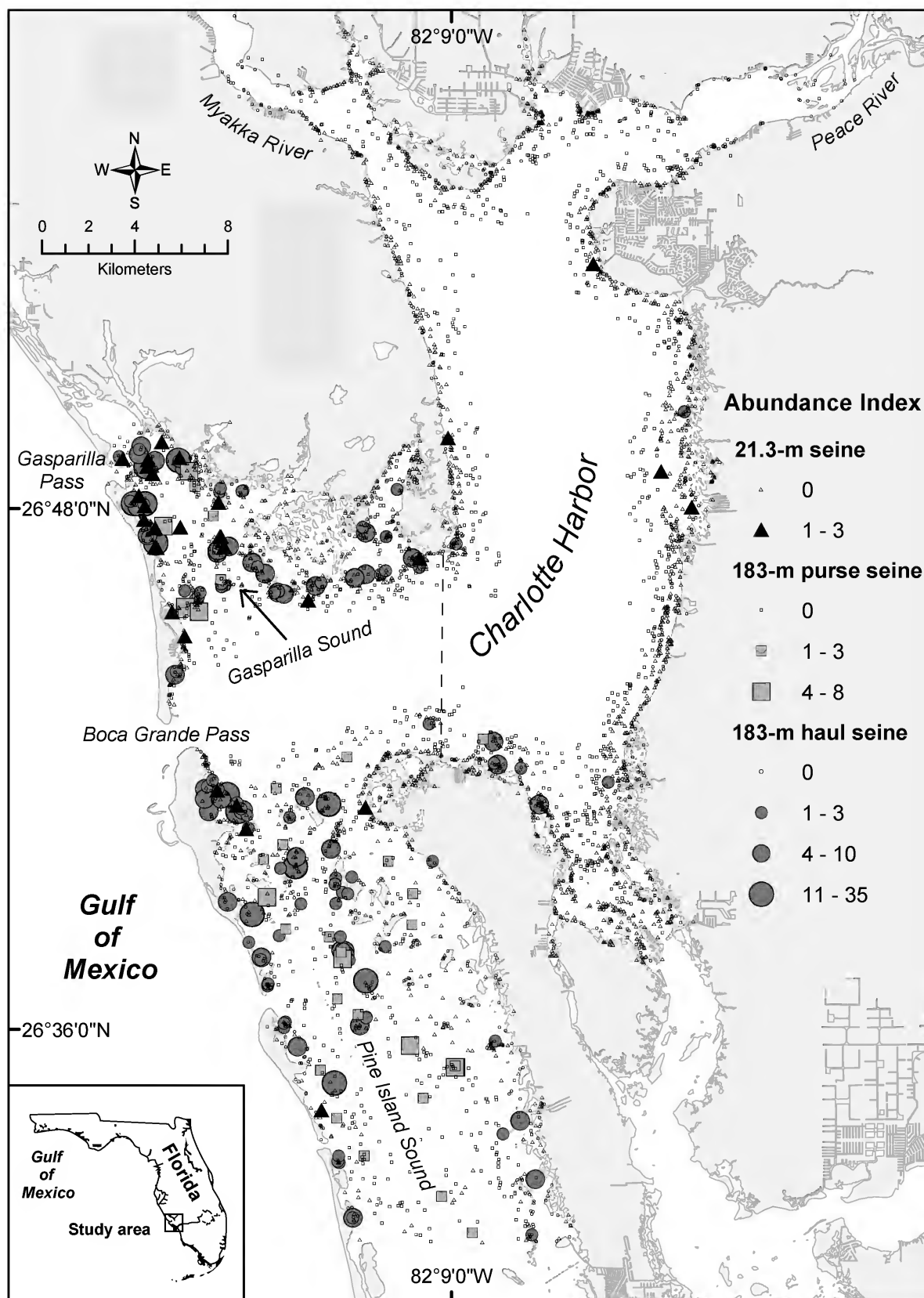


Figure 1. Distribution and relative abundance (abundance index = number of fish haul⁻¹) of juvenile gag in Charlotte Harbor, Florida. Samples ($n = 4,480$) were collected throughout the estuary, but most (95%) individuals were captured in Gasparilla and Pine Island sounds (areas west of dotted line).

TABLE 1

Summary of samples collected from 1996 to 2002 in Charlotte Harbor, Florida. The 2 sample regions are separated by the dotted line in Figure 1. (f) = number of samples that captured gag.

Gear	Eastern Charlotte Harbor		Gasparilla & Pine Island sounds		Total	
	Total samples	No. of gag (f)	Total samples	No. of gag (f)	Total samples	No. of gag (f)
21.3-m seine	1,192	7 (4)	872	33 (23)	2,064	40 (27)
183-m haul seine	712	33 (8)	644	582 (121)	1,356	615 (129)
183-m purse seine	530	1 (1)	530	82 (34)	1,060	83 (35)
Total	2,434	41 (13)	2,046	697 (178)	4,480	738 (191)

gag encounter when they move into estuaries throughout their range (Keener et al. 1988, Ross and Moser 1995). Gag spawn principally during February and March in the GOM (Hood and Schlieder 1992, Collins et al. 1998). Larvae remain in the plankton for about 40 d, and juveniles typically settle in temperate estuarine habitats in April and May (Keener et al. 1988, Ross and Moser 1995, Collins et al. 1998, Fitzhugh et al. 2005). Our data indicate that juvenile gag also moved into subtropical Charlotte Harbor and settled during April and May.

Due to the shape and hydrologic regime of Charlotte Harbor (rivers located far from passes and expansive polyhaline sounds), juvenile gag of various size classes were concentrated in high-salinity areas near Gasparilla and Boca Grande passes but also inhabited shallow areas in Gasparilla and Pine Island sounds several kilometers away from the GOM. In contrast, previous research determined that juvenile gag in temperate estuaries were concentrated in tidal creeks and seagrass beds near inlets (Ross and Moser 1995, Mullaney and Gale 1996, Koenig and Coleman 1998, Heinisch and Fable 1999). Exclusive use of polyhaline areas in estuaries by different size-classes has typically been attributed to low mobility during estuarine residency (Koenig and Coleman 1998, Heinisch and Fable 1999). However, it is unclear whether distribution is dependent solely upon settlement patterns or if survival decreases in lower salinities.

Within the polyhaline areas of estuaries, gag have been collected near seagrass beds, oyster-shell habitats, mangroves, seawalls, and jetties (Hastings 1979, Bullock and Smith 1991, Mullaney and Gale 1996, Koenig and Coleman 1998, present study). In Charlotte Harbor, juveniles were most abundant where water depths were >1 m on seagrass-covered shoals and along mangrove-lined shorelines—the dominant habitats in Gasparilla and Pine Island sounds. In estuaries where seagrasses are absent, juveniles typically have been collected from oyster-shell habitats in high-salinity tidal creeks (Mullaney and Gale

1996). Therefore, high-salinity habitats that provide structure appear to be preferred by juvenile gag during their estuarine residency throughout their range.

One habitat that has received little attention, but provides considerable structure and large areas of suitable habitat for juvenile gag, is fringing mangroves. A consistent number (low s_x for shoreline, see Figure 4) of juvenile gag were collected along fringing mangroves in this study. The dominant species of fringing mangrove in Charlotte Harbor is the red mangrove, which provides structure for fish assemblages in the form of prop roots and overhanging branches that extend into the water away from the shoreline (Thayer et al. 1987, Ley et al. 1999, Poulakis et al. 2003). Because of the large area (ca. 4,120 m²) and multiple habitats (e.g., seagrass beds, fringing mangroves) encompassed by the haul seine, the exact habitat where juvenile gag resided could not be determined using this gear. However, a hook-and-line study that targeted common snook (*Centropomus undecimalis*) captured juvenile gag as bycatch (D.A. Blewett, unpublished data, Fish and Wildlife Research Institute, Charlotte Harbor Field Laboratory). During hook-and-line sampling, juvenile gag were extracted from among red mangrove prop roots, providing evidence that they use fringing red mangrove habitats.

Studies conducted in temperate estuaries have indicated that the passage of cold fronts in September and October trigger the egress of juvenile gag from estuarine waters to open-ocean waters (Ross and Moser 1995, Koenig and Coleman 1998). Our data showed that juveniles began to decline in abundance throughout Charlotte Harbor from October to December. Before dispersing offshore, juvenile gag appeared to first move to deeper open waters within the estuary during October and November, as indicated by the increased number of juvenile gag captured in the purse seine, which samples deeper habitats away from shore. Although Charlotte Harbor becomes affected by cold fronts in September and October, the effects of those

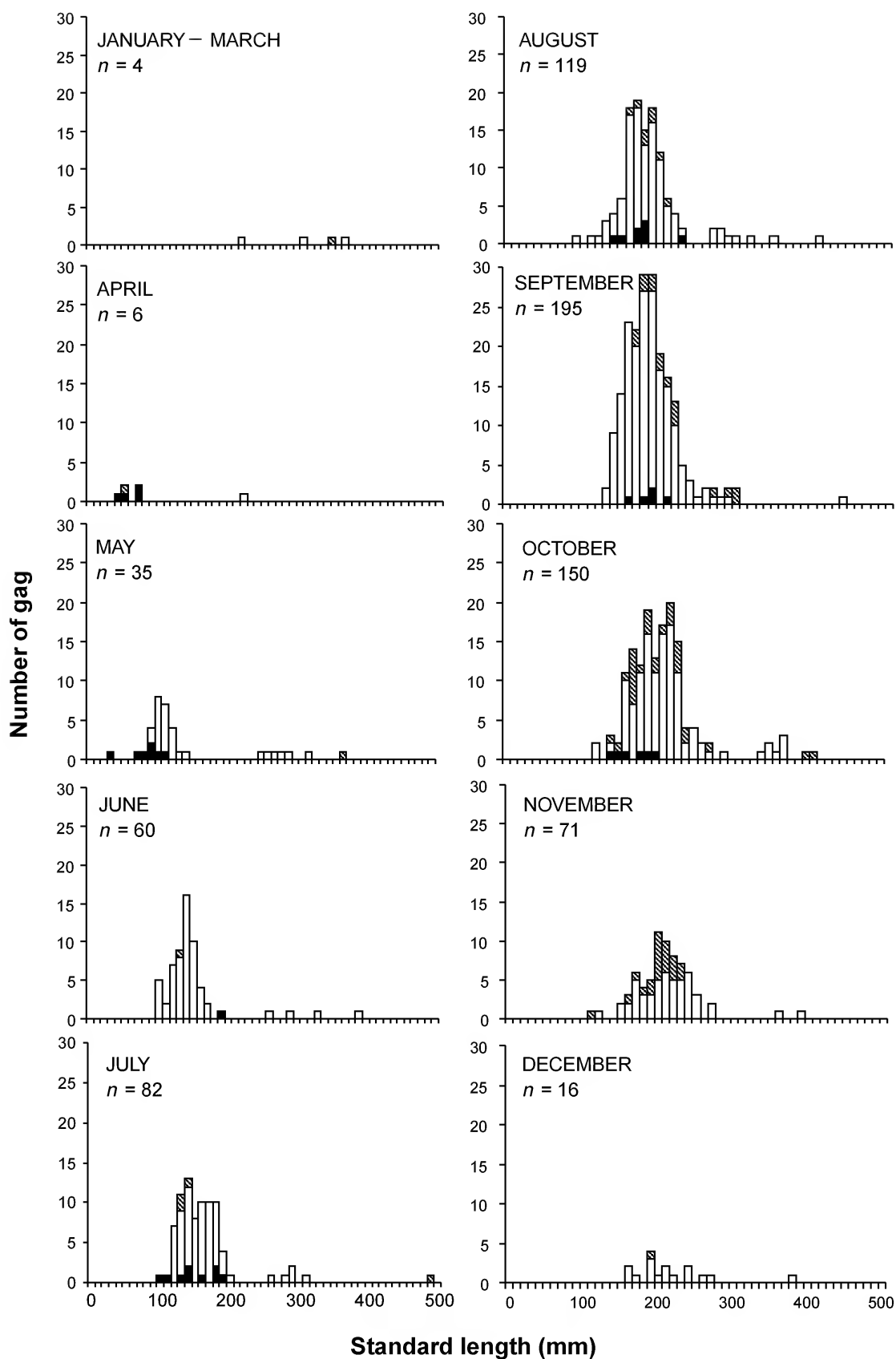


Figure 2. Monthly size distribution of juvenile gag in Charlotte Harbor, Florida (1996–2002). Black = 21.3-m seine, White = 183-m haul seine, Hatched = 183-m purse seine.

TABLE 2

The significant ($\alpha < 0.01$) variables identified by the general linear model analysis as contributing to the abundance of juvenile gag captured in the 183-m haul seine in Gasparilla and Pine Island sounds from May to December.

Source	df	Sum of squares	F	P	r ²
Model	17	56.82	8.10	< 0.0001	0.25
Month	7	10.67	3.70	0.0007	
Year	6	17.51	7.07	< 0.0001	
Geographic location	1	3.91	9.48	0.0022	
Shoreline vs. shoal	1	3.79	9.18	0.0026	
Water depth	1	12.62	30.59	< 0.0001	
Seagrass percent cover	1	8.71	21.12	< 0.0001	
Error	407	167.90			
Corrected total	424	224.72			

cold fronts are milder than at higher latitudes. Therefore, because juvenile gag remain in subtropical estuaries like Charlotte Harbor longer than they do in temperate estuaries, they may attain larger sizes before egressing.

Movement toward the ocean is enhanced by cold fronts, but these fronts are probably not the only cue used by gag. Previous studies have suggested that a few individuals may begin egressing to open ocean waters before water temperatures are lowered by cold fronts. For example, in Bogue Sound, North Carolina, and St. Andrews Bay, Florida, juveniles were observed along jetties in inlets several weeks before the first cold front (Ross and Moser 1995, Heinisch and Fable 1999). Similarly, near Charlotte Harbor, juvenile gag were observed near rock outcroppings on the GOM side of Boca Grande Pass during August in waters less than 5 m deep (J.P. Casey, pers. obs.). It is unknown whether these individuals settled out in these habitats or moved there after first settling in the estuary.

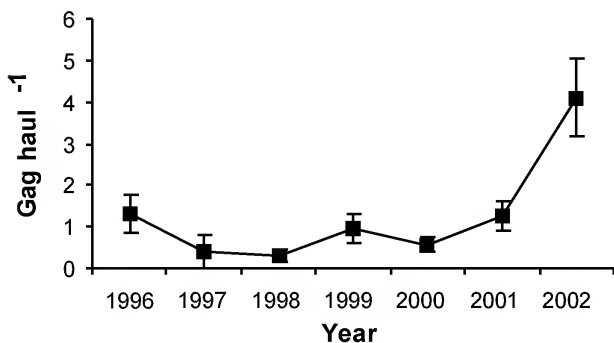


Figure 3. Annual mean relative abundance (abundance index = number of fish haul⁻¹) of juvenile gag captured in the 183-m haul seine from May to December in Gasparilla and Pine Island sounds (mean \pm s_x).

Although most juveniles egress to the GOM during their first winter, some individuals remain in estuaries for a second year or possibly return to their respective estuaries after moving into the GOM (Heinisch and Fable 1999, present study). Heinisch and Fable (1999) hypothesized that some fish remained in temperate St. Andrews Bay, Florida, during winter because of the great depth (19.8 m) in the inlet, but in Charlotte Harbor young gag have been collected during winter in relatively shallow water (≤ 3.3 m). Heinisch and Fable (1999) also suggested that larger juveniles migrate offshore and then return to their respective estuaries. Future studies would be necessary to understand the extent to which this may occur. One method that could be used to determine the movement between estuaries and offshore habitats is chemical markers within otoliths (Hanson et al. 2004).

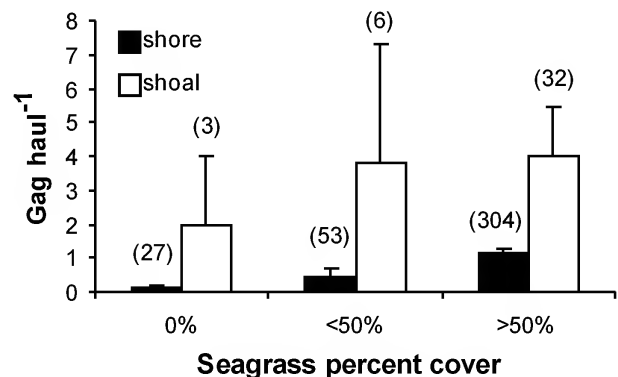


Figure 4. Mean relative abundance (abundance index = number of fish haul⁻¹) of juvenile gag captured with the 183-m haul seine from May to December in Gasparilla and Pine Island sounds by habitat (mean \pm s_x). Shore habitats included mangrove and beach shorelines, and shoal habitats included sandbars and oyster bars. Seagrass percent cover included up to three of the seagrass species found in Charlotte Harbor. The number in parentheses indicates the number of samples taken in each habitat.

In conclusion, the gag is an economically important reef species that is dependent on estuarine habitats during its early-life stages (Keener et al. 1988). Juvenile gag are distributed in the high-salinity areas of estuaries, and the period of settlement is similar in temperate and subtropical areas. However, gag remained in subtropical Charlotte Harbor longer and egressed at a larger size than in estuaries at higher latitudes. Habitat use by juvenile gag within the high-salinity areas of Charlotte Harbor was greatest on shallow seagrass shoals, but red mangrove-lined shorelines represent a suitable habitat not previously reported for this species. Interannual variability in gag abundance was evident in Charlotte Harbor, with 2002 having a stronger year-class than the other years of this study. Variability in young-of-the-year abundances may be attributed to fluctuations in factors such as fecundity of the offshore population, larval mortality, larval transport to the estuary due to winds and associated currents, and survival rates within the estuary (Keener et al. 1988, Epifanio and Garvine 2001, Paperno 2002, Fitzhugh et al. 2005). This study describes specific locations, habitat types, and interannual patterns of abundance within the Charlotte Harbor estuary that can be used to gauge future changes that may result from natural (e.g., hurricanes) or anthropogenic alterations to water quality and habitat.

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BREEDING SEASON AND MOLT CYCLE OF THE FIDDLER CRAB *UCA RAPAX* (BRACHYURA, OCYPODIDAE) IN A SUBTROPICAL ESTUARY, BRAZIL, SOUTH AMERICA

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ABSTRACT This is the first account of the breeding season and molt cycle of *Uca rapax* on the Brazilian coast during a one-year period (April 2001–March 2002). At 2 sites, the Itamambuca and Ubatimirim mangrove forests, 2 collectors captured crabs once a month at low tide for 15 minutes by the catch-per-unit-effort procedure, digging into the sediment and removing the crabs. The gonad-development stages of crabs of both sexes were determined by direct observation, and the molt stage was estimated from the hardness of the tegument. Crabs with developed gonads were found mostly in warmer seasons, with ovigerous females occurring mainly in summer and autumn. The reproductive cycle is seasonal. Recently molted individuals were collected in relatively higher numbers for juveniles than for adult crabs.

INTRODUCTION

The reproductive strategy of brachyuran crabs is extremely diversified, ultimately shaped to maximize egg production and offspring survivorship, thus increasing the chances for preservation of the species (Hartnoll and Gould 1988). The reproductive period for many brachyurans can be estimated by observing gonad maturation at the macro- or microscopic levels and from the frequency of ovigerous females in the population (e.g., Wolfrath 1993, Emmerson 1994, Mouton and Felder 1995, Costa and Negreiros-Fransozo 2003, Colpo and Negreiros-Fransozo 2003, Litulo 2004, 2005a, 2005b). The reproductive period results from a complex interaction between internal and external factors, leading to intra- and inter-specific variation in the duration of the reproductive season (Sastry 1983).

Many ocypodid crabs have seasonal reproduction, as observed in *Uca lactea* (de Haan, 1835) studied by Yamaguchi (1971), in *Uca pugilator* (Bosc, 1802) and *Uca pugnax* (Smith, 1870) studied by Christy (1982), and *Uca thayeri* Rathbun, 1900 studied by Salmon (1987). The limited reproductive season in semi-terrestrial crabs might be related to changes in the temperature and photoperiod and the availability of food resources (Pillay and Ono 1978). The availability of food for body maintenance, somatic growth and reproduction of the adult crabs, and for growth and survival of the larval and/or juvenile stages is assumed to be the most important factor (Sastry 1983) in synchronization and coordination of reproductive activity in a given habitat.

Mangrove ecosystems are highly productive environments, hospitable for feeding, growth, and reproduction of many species of crabs, shrimps, fishes, and other animals (Schaeffer-Novelli 1995). In these ecosystems, fallen mangrove leaves provide most of the organic matter deposited in the sediments. Deposit-feeding ocypodid crabs of the genus *Uca* feed on the organic matter, including the endofauna that are sorted out from the substrate. Their actual food supply depends on the ecosystem productivity, microbial activity, substrate texture, and tidal action (Murai et al. 1982, Twilley et al. 1995, Moura et al. 1998). There are about 100 species of fiddler crabs worldwide, most of them included in 2 distinct morphological categories with different morphology, zoogeography, and behavior: the broad-front species and the narrow-front species (Crane 1975, Christy and Salmon 1984, Rosenberg 2001). There are about 10 species of fiddler crabs typically found in Brazilian mangroves: *Uca burgersi* Holthuis, 1967; *Uca cumulanta* Crane, 1943; *Uca leptodactyla* Rathbun, 1898; *Uca mordax* (Smith, 1870); *Uca rapax* (Smith, 1870); *Uca uruguayensis* Nobili, 1901; *Uca victoriana* (von Hagen, 1987); *Uca vocator* (Herbst, 1804); *Uca thayeri* Rathbun, 1900; and *Uca maracoani* (Latreille, 1802–1803) (Melo 1996). A peculiar morphological feature separating these species into 2 groups is the size of the carapace front. *Uca burgersi*, *U. cumulanta*, *U. leptodactyla*, *U. mordax*, *U. rapax*, *U. uruguayensis*, *U. victoriana*, *U. vocator* and *U. thayeri* have a broad front, while *U. maracoani* has a narrow front.

Among the species studied here, *U. rapax* is one of the most abundant species of the genus *Uca* in the Brazilian

mangroves. It burrows into mud or muddy sand and feeds on organic matter in the sediment of mangroves along the northern coast of the State of São Paulo, Brazil. According to Melo (1996), *U. rapax* is distributed throughout Florida, the Gulf of Mexico, the Antilles, Venezuela, and Brazil (from the states of Pará to Santa Catarina).

This study investigates the breeding season and molt cycle of *U. rapax* from the Itamambuca and Ubatumirim mangrove forests near Ubatuba on the northern coast of São Paulo, Brazil. The studies are based on the frequency of gonad and molt stages and the ratio of ovigerous females. Although located close to each other, the study sites have distinct landscapes and hydrological features that determine the vegetation community. The vegetation in the Itamambuca mangrove (23°24'4"S, 45°00'7"W) consists of only *Laguncularia racemosa* (Linnaeus). In the Ubatumirim mangrove (23°20'17.8"S, 44°53'22"W) the vegetation is mostly *L. racemosa* with some *Avicennia shaueriana* Stapf. and Leech (Negreiros-Fransozo, pers. comm.). The Itamambuca mangrove is a highly productive ecosystem with hydrology and sediment characteristics that retain minerals and a rich environment suitable for development of fiddler crab populations (Colpo 2001). As described by Castiglioni and Negreiros-Fransozo (2004), these 2 mangroves have distinctly different sediment organic matter content and texture as well as river and burrow salinities.

MATERIAL AND METHODS

Crabs were collected monthly by 2 people from April 2001 through March 2002 in both mangroves, using the procedure of catch per unit effort (cpue). Over 15 min time periods during low tides (spring tide), crabs were removed from their burrows by digging to the end of each burrow with diving knives. Additional collections were made in August through December 2002, using the same procedure attempting to locate ovigerous females.

Crabs were counted, sexed, and measured (carapace width (CW) to the nearest 0.01 mm), and females were checked for eggs. Ovigerous females were preserved individually in 70% ethanol.

We determined the relative frequency of ovigerous females over the course of the year. The stages of embryonic development were classified as initial, intermediate, or final, according to the relative proportion of yolk content and the appearance of eyes and appendage buds in the embryo (see Costa and Negreiros-Fransozo 1998 for details). A multinomial proportions analysis (Curi and Moraes 1981) with a 5% significance level was used to examine reproductive seasonality. From this analysis we

considered autumn as April, May, and June; winter as July, August, and September; spring as October, November, and December; and summer as January, February, and March.

The size of ovigerous females was compared between the populations by Student's *t* test ($\alpha = 0.05$; Zar 1996). The gonad development stages were analyzed in each sex. The carapace in the dorsal region was removed, and the shape, size, and color of the gonads were observed under a stereomicroscope. The female gonads were classified in 6 developmental stages: spent = SP; advanced = AD; developed = DE; developing = DI; rudimentary = RU; and immature = IM. Five stages were used for males: spent = SP; developed = DE; developing = DI; rudimentary = RU and immature = IM. This procedure was modified from Haefner (1976), Abelló (1988), Choy (1988) and Costa and Negreiros-Fransozo (1998). Comparisons of the gonad proportion between seasons in each sex were performed using a multinomial proportions analysis (Curi and Moraes 1981) to determine the reproductive period.

Fiddler crabs were arranged in 2 groups: juvenile or immature crabs (specimens with immature or rudimentary gonads) and adult or mature crabs (specimens with developing, developed, advanced, or spent gonads). Comparisons of the immature and mature crabs between seasons in each sex were performed using a multinomial proportions analysis (Curi and Moraes 1981). The reproductive period was determined using data for the frequency of mature males and females over the year (Costa and Negreiros-Fransozo 1998, Mantelatto and Fransozo 1999).

The air and burrow temperatures were measured monthly, with 3 replicates at each site, and were compared by ANOVA among seasons and sites ($\alpha = 0.05$; Zar 1996). The degree of association among crabs with developed gonads and environmental factors (air and burrow temperatures) was assessed using Pearson's correlation ($\alpha = 0.05$; Zar 1996).

The molt stages were described based on Warner (1977) and Abelló (1988) as follows: A) post-recent molt = carapace very flexible and without calcification; B) post-advanced molt = onset of calcification; brittle carapace but more resistant and with a consistency similar to cardboard; C) intermolt = carapace fully calcified, with a leathery consistency; D) pre-molt = a new exoskeleton present inside the old one and the molt lines emerging in the pterigostomial region; and E) molt = exact moment of the change or exit of the animal from the old exoskeleton.

Following this scheme, the molt stages were grouped in 2 phases: molt activity (A, B, and D stages) and intermolt (C stage). The proportions of the 2 stages were compared between seasons using the multinomial proportions analysis (Curi and Moraes 1981). We analyzed the molt

frequency in each sex by size class (CW) for both mangroves.

RESULTS

During the study period, a total of 1,294 fiddler crabs were collected at Itamambuca: 667 males and 627 females. Eight ovigerous females were collected in the autumn which corresponds to 2.22% of all adult females. In the Ubatumirim mangrove, during the summer, a total of 2,107 specimens were collected: 1,117 males and 990 females with 20 ovigerous females (3.03%). Most of the ovigerous females collected from both mangroves bore eggs in the final embryonic developmental stage. The additional collection taken in November 2002 comprised 27 ovigerous females from Itamambuca and 67 from Ubatumirim. Most of the ovigerous crabs eggs were in the final developmental stage. When collected, the crabs had emerged from burrows and were moving freely on the substrata. Ovigerous females ranged from 14.2 to 24.2 mm CW at Itamambuca and 10.2 to 21.3 mm CW at Ubatumirim. The mean size of ovigerous females from Itamambuca (19.5 ± 3.3 mm; mean $\pm s$) was larger than ovigerous females from Ubatumirim (16.2 ± 3.2 mm; mean $\pm s$) (Student t test; $P < 0.05$).

Males with developed gonads were found in all seasons, but significantly more males in this condition were found in the summer and autumn at Itamambuca ($P < 0.05$) (Table 1). Males with developing gonads were found in all seasons, but significantly more were found in the spring and summer at Ubatumirim (ANOVA; $P < 0.05$) (Table 2).

Females with developing and developed gonads were found in most of the samples, except during the winter at Ubatumirim. Females with advanced gonads occurred only during the summer at both sites ($P < 0.05$). In both populations there were many females with spent gonads in the autumn and winter (ANOVA; $P < 0.05$), unlike in the other seasons (Tables 1 and 2).

In the Itamambuca mangrove, mature males were found in higher frequencies during autumn, spring, and summer, whereas mature females increased only during summer (Table 3) (ANOVA; $P < 0.05$). At Ubatumirim, mature males were frequent in all seasons of the year, and mature females were frequent during spring and summer (Table 4) (ANOVA; $P < 0.05$).

The mean air temperature was similar between mangrove sites and did not differ markedly through seasons (ANOVA; $P < 0.05$). The lower temperatures were registered during autumn (ANOVA; $P < 0.05$) (Table 5). The mean temperature inside the burrows of *U. rapax* did not

TABLE 1

Frequency (%) of the gonad stages (SP = spent; AD = advanced; DE = developed; DI = developing; RU = rudimentary; IM = immature) for male and female *Uca rapax* during the seasons (Au = Autumn; W = Winter; Spr = Spring; Su = Summer) in the Itamambuca mangrove.

Stages	Seasons			
	Au	W	Spr	Su
Males				
SP	17.0 a AB	18.0 a A	15.0 a BC	15.0 a BC
DE	15.0 a C	5.0 bc C	0.5 c C	12.0 ab BC
DI	34.0 a A	35.0 a A	35.0 a B	37.0 a A
RU	3.0 c C	15.0 b BC	27.0 ab AB	30.0 a AB
IM	29.0 a AB	27.0 a AB	22.0 a AB	5.0 b C
Females				
SP	55.0 a A	41.0 ab A	15.0 c B	35.0 b A
AD	0.6 b D	0.0 b BC	0.0 b C	11.0 a BC
DE	2.0 b CD	3.0 c BC	7.0 a B	9.0 a BC
DI	8.0 ab C	3.0 b BC	15.0 a B	23.0 a AB
RU	2.0 c CD	6.0 bc C	29.0 ab A	15.0 a BC
IM	31.0 a B	46.0 a A	32.0 a A	7.0 b C

Note: lower case letters correspond to the comparisons in each gonad stage among the seasons; capital letters correspond to the comparisons among the gonad stages in each season. Values with at least one letter in common did not differ statistically ($\alpha = 0.05$).

differ between sites in a same season but reached maximum values during the summer at both sites (ANOVA; $P < 0.05$) (Table 5).

The relative frequency of mature males and females tended to increase with increasing air temperature (Itamambuca: $r^2 = 0.71$ in males; $r^2 = 0.53$ in females; Ubatumirim: $r^2 = 0.98$ in males; $r^2 = 0.66$ in females; $P < 0.05$) (Figure 1).

Throughout the year, significantly more (ANOVA; $P < 0.05$) specimens were in the intermolt than molt stages for

TABLE 2

Frequency (%) of the gonad stages (SP = spent; AD = advanced; DE = developed; DI = developing; RU = rudimentary; IM = immature) for male and female *Uca rapax* during the seasons (Au = Autumn; W = Winter; Spr = Spring; Su = Summer) in the Itamambuca mangrove.

Stages	Seasons			
	Au	W	Spr	Su
Males				
SP	37.0 ab A	43.0 a A	28.0 bc A	24.0 c AB
DE	3.0 a B	0.7 a C	2.0 a C	12.0 a BC
DI	14.0 b C	20.0 b B	33.0 a A	33.0 a A
RU	12.0 b C	17.0 ab B	23.0 a AB	21.0 ab ABC
IM	33.0 a A	20.0 b B	13.0 b B	10.0 b C
Females				
SP	11.0 ab B	20.0 a C	8.0 b B	8.0 b B
AD	0.0 a C	0.0 a B	0.0 a C	6.0 b B
DE	3.0 ab C	0.0 b B	8.0 a B	18.0 a BC
DI	6.0 b BC	0.4 c B	28.0 a A	19.0 a C
RU	43.0 ab A	41.0 a A	31.0 b A	8.0 c A
IM	36.0 ab A	39.0 a A	24.0 b A	11.0 c BC

Note: lower case letters correspond to the comparisons in each gonad stage among the seasons; capital letters correspond to the comparisons among the gonad stages in each season. Values with at least one letter in common did not differ statistically ($\alpha = 0.05$).

both populations (Figures 2 and 3). There were no significant differences between sexes in the molt activity, except for males in Itamambuca (Figure 2). Smaller crabs of both sexes molted more often (Figure 4).

Figure 5 shows the frequency of molt activity of *U. rapax* in relation to gonadal development stages for each sex. The recently molted stage A (see Materials and Methods) was observed in male crabs that had immature gonads and females with immature and rudimentary gonads in the Itamambuca mangrove population. At Ubatumirim,

TABLE 3

Frequency (%) of immature and mature *Uca rapax* by season in the Itamambuca mangrove.

Seasons	Males		Females	
	Immature	Mature	Immature	Mature
Autumn	37.7 ab	62.3 a	38.8 b	61.2 b
Winter	50.6 a	49.4 b	61.4 a	38.6 c
Spring	37.0 ab	63.0 a	46.2 b	53.8 b
Summer	35.6 b	64.4 a	21.9 c	78.1 a

Note: lower case letters correspond to the comparison between each demographic category for each sampling season. Values with at least one letter in common did not differ statistically ($\alpha = 0.05$).

TABLE 4

Frequency (%) of immature and mature *Uca rapax* by season in the Itamambuca mangrove.

Seasons	Males		Females	
	Immature	Mature	Immature	Mature
Autumn	45.0a	55.0b	79.3a	20.7b
Winter	36.6ab	63.4ab	79.9a	20.1b
Spring	36.8ab	63.2ab	55.5b	44.5a
Summer	31.2b	68.8a	59.5b	40.5a

Note: lower case letters correspond to the comparison between each demographic category in each sampling season. Values with at least one letter in common did not differ statistically ($\alpha = 0.05$).

this molt stage was observed in males with rudimentary and spent gonads, but it was not observed in any females. Male crabs in the post-advanced molt stage (B) have been found in all gonad stages from both mangroves. However, this molt stage was not observed in female crabs with advanced gonads from Itamambuca, or in females with advanced and developed gonads from Ubatumirim.

DISCUSSION

In the main systematic sampling period, a small number of ovigerous females were found in Itamambuca and Ubatumirim mangroves. However, additional ovigerous females were collected in the additional samples (August–December 2002), and most of them had emerged from and were moving around the burrows and carrying eggs in the late embryonic stage. According to Salmon (1987), females of broad-fronted fiddler crabs such as *U. rapax* can incubate their eggs underground to protect them from extreme environmental conditions. This provides

TABLE 5

Comparison of mean ($\pm s$) temperature in °C between year seasons in the mangroves. s = standard deviation.

Seasons	Sites			
	Itamambuca		Ubatumirim	
	Air temperature	Burrows temperature	Air temperature	Burrow temperature
Autumn	24.6 \pm 5.36 b	25.00 \pm 4.52 bc	25.00 \pm 1.10 b	24.70 \pm 2.15 b
Winter	30.10 \pm 6.02 a	22.80 \pm 0.79 c	28.20 \pm 2.79 ab	26.80 \pm 2.53 b
Spring	31.10 \pm 5.76 a	27.50 \pm 0.91 bc	27.80 \pm 2.73 ab	25.10 \pm 3.03 b
Summer	32.90 \pm 1.78 a	31.60 \pm 2.50 ab	32.40 \pm 2.91 a	31.60 \pm 4.45 a

Note: Values with at least one letter in common within a column did not differ statistically (ANOVA; $\alpha = 0.05$).

a uniform environment, thus promoting synchrony in embryonic development and larval hatching. Christy and Salmon (1984), Murai et al. (1987), and Henmi (2003) also observed such behavior in *Uca pugilator* (Bosc, 1802), *Uca lactea* (DeHaan, 1875), and *Uca perplexa* (H. Milne Edwards, 1837), respectively. The ovigerous females had large broods, remained in their burrows during the entire incubation period, and did not feed during this phase. We infer that the individuals of *U. rapax* in the mangroves studied may have been searching for a hatching area.

To maximize the probability of larval survival, where their eggs are ripe for hatching, many mangrove crabs travel the long distance to the water's edge during the night (Gifford 1962). Only ovigerous females of *U. rapax* with eggs in the final embryonic development stage were found during this study, probably because these females are

more active or exit their burrows to liberate the larvae during spring tide periods. Christy (1978) suggested that the synchronization of reproduction with tidal cycles in *Uca* species could be an adaptation to increase the probability that the planktonic larvae are carried back to the adults' environment by tidal currents.

In species of *Uca* with large broods, the females produce more eggs in a single spawn, but they cannot carry eggs continuously. This is probably because of the vulnerability of the large egg masses to stress and desiccation. Females of these species do not feed enough during the incubation period to develop new oocytes internally. On the other hand, species with small broods produce fewer eggs each spawn but can develop broods continuously; their egg mass is protected, and the females can feed during incubation to develop a new brood (Henmi 1989,

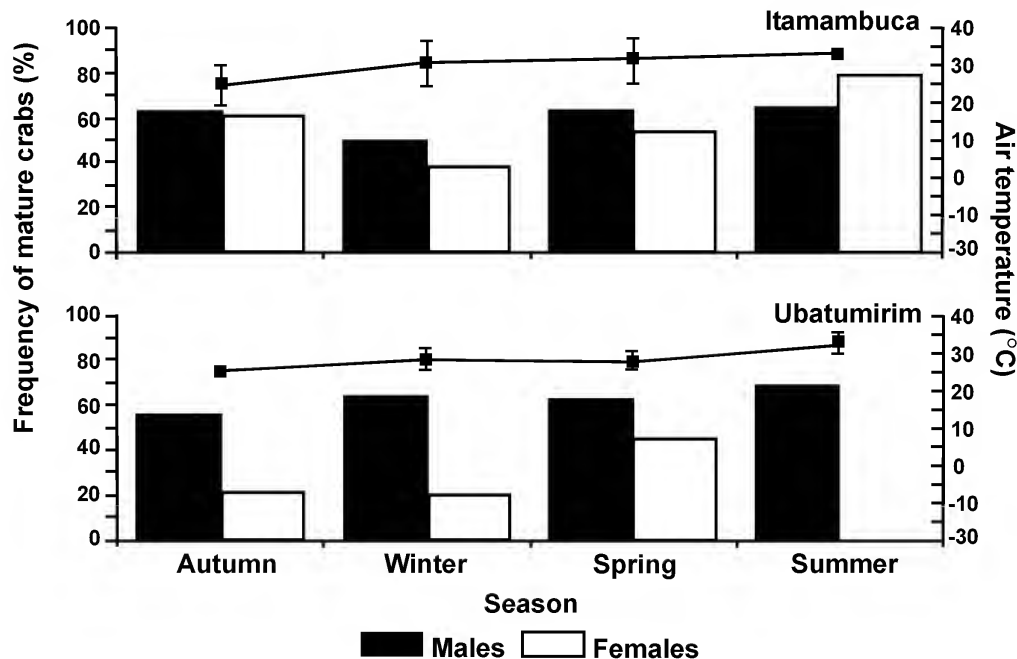


Figure 1. Frequency of mature fiddler crabs (males and females) and air temperature (°C; mean $\pm s_x$) in both mangroves seasonally. s_x = standard error.

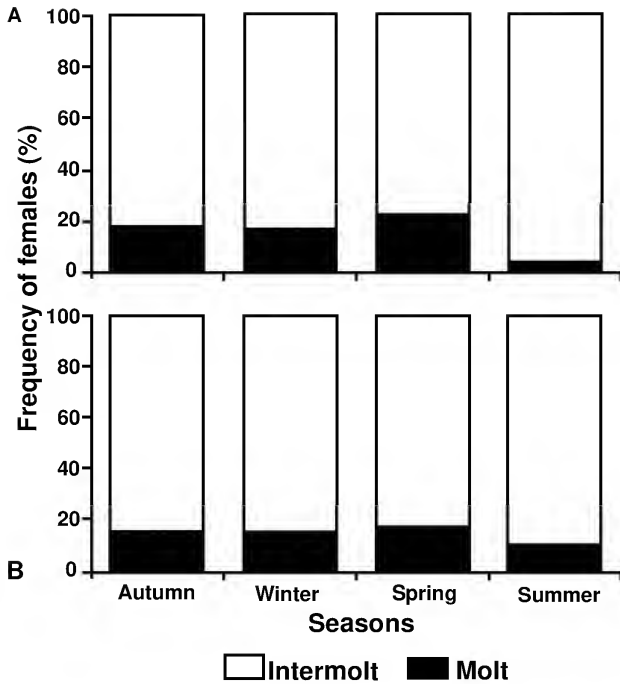


Figure 2. *Uca rapax* in Itamambuca mangrove: Plot of mean seasonal frequency of molt activity and intermolt for males (%) (A), females (B). All seasonal comparisons between molt and intermolt did not differ significantly ($P > 0.05$).

Henmi and Kaneto 1989). Because the egg mass of *U. rapax* does not remain completely covered by the abdomen, and also because no females were caught with eggs in initial and intermediate embryonic development, we suppose that the ovigerous females remain in their burrows during the incubation period. The ovigerous females collected had spent and empty gonads. These females probably do not bear a new brood immediately after larval hatching as in other *Uca* species as they probably do not feed during the incubation period and have no resources to produce new egg masses.

Fiddler crabs are typically adapted to live in hot climates. In the tropics, they are active year-round, and reproductively active crabs are found during all months, since environmental conditions are permanently favorable for feeding, gonad development, and larval release (Sastry 1983, Thurman 1985). In the subtropics, reproduction in some species is limited more by the dry season than by temperature. For a few species, usually those living in temperate zones, reproduction is controlled by temperature, by their distributional limits, or in some cases by intertidal zonation, e.g., the ocypodid crab *Macrophthalmus grandieri* A. Milne Edwards, 1867 studied by Emmerson (1994). Reproduction is restricted to the warmer months (summer in the south hemisphere) in fiddler crabs, whereas during the colder months (winter in the south hemisphere)

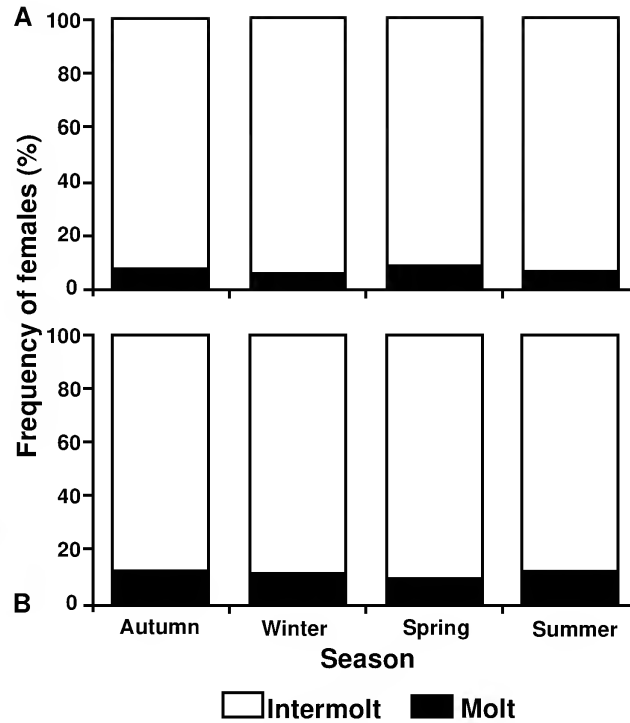


Figure 3. *Uca rapax* in Ubatumirim mangrove: Plot of mean seasonal frequency of molt activity and intermolt for males (%) (A), females (B). All seasonal comparisons between molt and intermolt did not differ significantly ($P > 0.05$).

they hibernate in their burrows (Crane 1975). Some investigators (Yamaguchi 1971, Christy 1982, Salmon 1987, Rodríguez et al. 1997) have observed the occurrence of reproduction during warmer months in *Uca* species. In both mangrove populations that we studied, the period of high reproductive activity in *U. rapax* occurred in the summer, but this species could also be found reproducing during other months, except in winter. Associations between temperature and reproduction may be related to better conditions for larval development, in terms of the availability of food or more favorable conditions for larval growth. However, in the case of tropical species with year-round procreation, reproduction may be associated with other factors, not only with temperature (Santos and Negreiros-Fransozo 1999, Costa and Negreiros-Fransozo 2003). Factors such as day length, food availability, rainfall and photoperiod have been indicated as other major modulators of reproduction in brachyurans (Conde and Díaz 1989, Zimmerman and Felder 1991, Flores and Negreiros-Fransozo 1998, Leme and Negreiros-Fransozo 1998, Negreiros-Fransozo et al. 2002, Cobo and Fransozo 2003, Litulo 2004).

The *U. rapax* populations of the Itamambuca and Ubatumirim mangroves had high proportions of crabs with developed and advanced gonads during the warmer seasons, which may be related to adequate conditions for

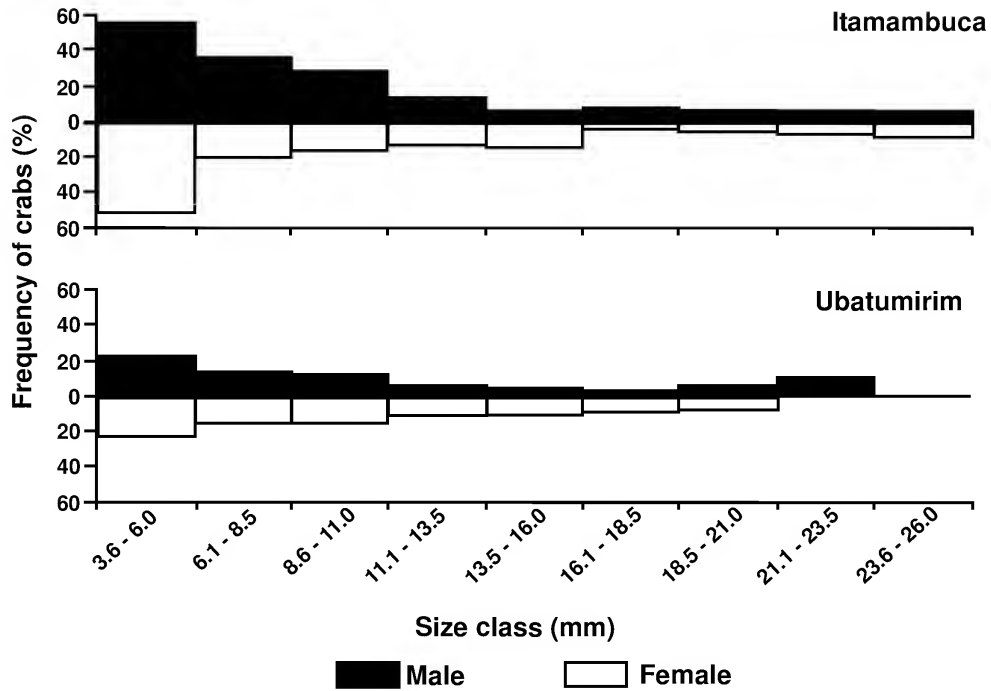


Figure 4. Frequency of molt activity (%) for male and female *Uca rapax* by size class (carapace width) in both mangroves.

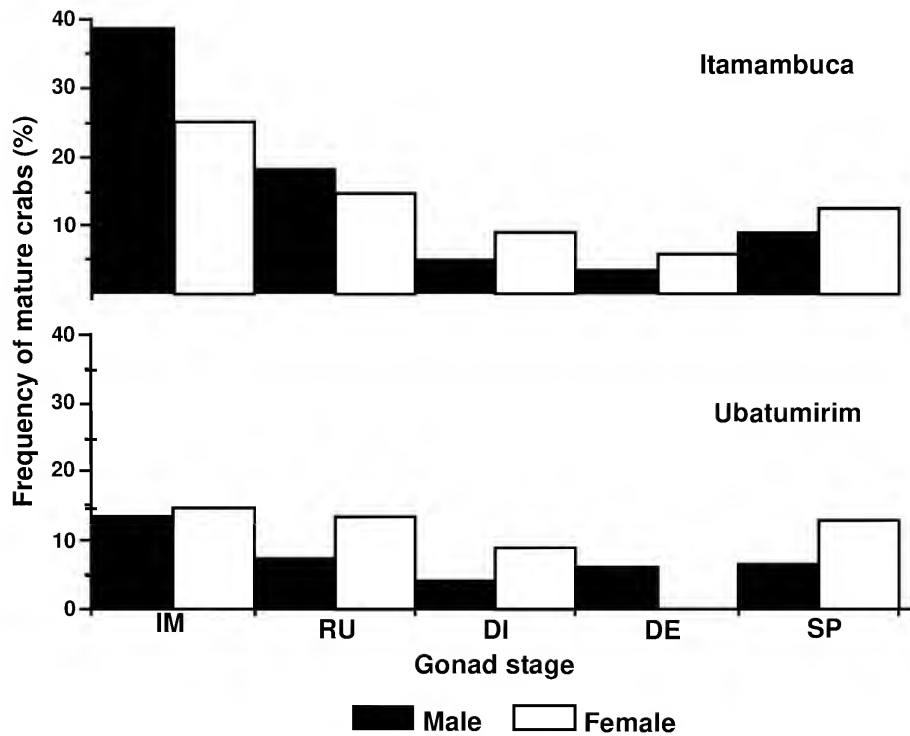


Figure 5. Frequency of molt activity (%) in relation to gonad stages for male and female *Uca rapax* in both mangroves. IM = immature, RU = rudimentary, DI = developing, DE = developed, and SP = spent.

the development and survival of the brood at these times. Haley (1970), studying the ocypodid *Ocypode quadrata* (Fabricius 1787) in Texas, observed that females with mature ovaries occurred in high proportions from April to August (spring–summer), suggesting that this period is one of intense reproductive activity. This may be related to day length, which stimulates ovarian maturation in immature females. Negreiros-Fransozo et al. (2002) investigated the biology of *O. quadrata* in a sandy beach at Ubatuba, Brazil and observed high reproductive intensity from October to May (spring, summer, and autumn). The higher abundance of females with fully developed gonads in this period was positively correlated with abiotic factors such as air temperature, water surface temperature, and precipitation.

The high intensity of molt activity in the first size classes can be explained by the direction of energy into growth until the crabs attain sexual maturity. After this phase, the frequency of the crabs in molt activity decreases, because energy resources become divided between molting and reproduction (Hartnoll 1988). After the pubertal molt, we observed many crabs in the process of molting, which mitigates against the hypothesis that a terminal molt occurs in *U. rapax* soon after sexual maturity.

The low incidence (under 30%) of sexually mature crabs in molt activity is usual for semi-terrestrial crabs. Moreover, fiddler crabs molt underground (Hyatt and Salmon 1978, Christy and Salmon 1984, Salmon 1987, Atkinson and Taylor 1988, Koga et al. 2000).

The antagonism between the reproductive process and growth is well known in crustaceans. The competition for energy resources required by one process or another leads to wide diversity in patterns of growth and reproduction (Hartnoll 1985, López-Greco and Rodríguez 1999). These patterns allow each species to maximize its reproductive potential within the limits of its genotypic plasticity (Hartnoll 1985). It can be assumed that the pattern of *U. rapax* results from the interaction between growth and reproduction. However, several aspects concerning the manner in which these antagonistic processes interact still requires investigation.

In all crustaceans, reproduction is dynamically related to the physical and chemical conditions of the organisms and to environmental conditions, food availability, and the presence of competitors or predators. The relative importance of the proximity of the factors that control reproductive activity can vary for different species in the same environment or in habitats with different characteristics (Sastry 1983). Differences like sediment organic matter content, river and burrow water salinity, and granular composition of the substrate (see Castiglioni and Negreiros-Fransozo 2005) appear to act directly or indirectly on aspects of the

populations. Reproduction is especially affected leading to variations in the process in different populations.

This is the first account of the breeding season and molt cycle of *Uca rapax* in Brazil. Further studies on fecundity, fertility, larval migrations, reproductive behavior, and feeding will add to our comprehension of the reproductive strategies of this fiddler crab.

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A COMPARISON OF FISH ASSEMBLAGES AMONG FIVE HABITAT TYPES WITHIN A CARIBBEAN LAGOONAL SYSTEM

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ABSTRACT Fish assemblages associated with patch reefs, rubble, seagrass, algal plain, and sandy habitats types were studied at St Croix's Southeastern barrier reef lagoon using underwater visual census techniques. Higher species richness and fish density were observed over patch reefs/rubble habitat followed by seagrass, algal plain, and unvegetated sandy habitat types. *Thalassoma bifasciatum*, *Haemulon flavolineatum*, and *Acanthurus chirurgus* were the most common fishes in highly structured habitat types (patch reef, rubble). *Halichoeres bivittatus*, *Sparisoma radians*, newly settled grunts (i.e., *Haemulon* spp.), and juveniles of *Ocyurus chrysurus* were mainly associated with vegetated habitat types (seagrass, algal beds), while *Xyrichtys martinicensis* and *Coryphopterus glaucofraenum* were common over unvegetated sandy habitat types. Cluster analysis among backreef lagoon habitat types based on the entire fish density data showed distinct associations of fish assemblages by habitat type, regardless of season. Fish assemblages in the more structured habitat types were similar to each other but different from unstructured vegetated, and unvegetated habitat types. These results suggest that differences in fish species richness and density in the backreef lagoon are related to habitat type. The ecological importance and need for protection of backreef lagoon habitat types are discussed in relation to their potential role as nurseries for many fish species.

INTRODUCTION

Nearshore ecosystems such as seagrass meadows, marshes, and mangrove lagoons supply many vital ecological functions in coastal waters, including shoreline protection, and nutrient cycling (Ogden and Gladfelter 1983, Parrish 1989). Most notably, these ecosystems provide food and refuge that supports a great abundance and diversity of fishes as well as shrimp, oysters, crabs, and other invertebrates (Ogden and Ziemann 1977, Shulman 1984, Shulman 1985, Parrish 1989). In the Caribbean, it has generally been accepted that mangroves and seagrass meadows form important nurseries for juveniles of several reef fish species (Ogden and Gladfelter 1983, Parrish 1989, Nagelkerken et al. 2000), and juvenile coral reef fishes have been frequently observed in mangroves and seagrass meadows in the Caribbean (e.g., Baelde 1990, Sedberry and Carter 1993, Appeldoorn et al. 1997, Lindeman et al. 1998, Nagelkerken et al. 2000). The adults of these species have been observed on reef environments or in offshore waters, suggesting the migration of juvenile from the mangroves and seagrass beds to the reef or deeper waters at a certain age (Ogden and Ehrlich 1977, Weinstein and Heck 1979, Rooker and Dennis 1991, Appeldoorn et al. 1997, Lindeman et al. 1998, Nagelkerken et al. 2000). Although numerous studies have been done on mangrove, seagrass, and coral reef systems, only recently researchers have investigated the connectivity among these coastal ecosystems (Sedberry and Carter 1993, Nagelkerken et al.

2000, Adams and Ebersole 2002). Comparisons of nursery value among nearshore habitat types have usually focused on a single habitat (i.e., mangrove or seagrass) (Robblee and Ziemann 1984, Baelde 1990, Rooker and Dennis 1991) even though individual species may use many different habitats. Furthermore, embayments and lagoons often not only contain mangroves and seagrass meadows, but a variety of other shallow-water habitats like algal plains, areas with bare sediment, sand-rubble zones, or patch reefs. Seagrass meadows and mangroves may be less important as nurseries in regions where animals use alternative habitats successfully. Few studies have quantified the proportions of reef fishes that pass through these nursery habitats, and information concerning other habitats that can be used as alternative nurseries are lacking. Thus, linkages of fishes between these backreef lagoon habitats remain largely unknown (Ogden and Gladfelter 1983, Birkeland 1985, Parrish 1989). Therefore, this study addresses the following questions: 1) Does species composition and abundance differ among backreef lagoon habitat types? 2) Which habitat types are used as nurseries by selected fish species? 3) Which backreef lagoon habitat types are utilized more by a fish species when multiple nursery habitat types are present? 4) Do fish species show an ontogenetic shift from nursery habitat types to other backreef lagoon habitat types? 5) Do closely related fish species show similar seasonal patterns in habitat use?

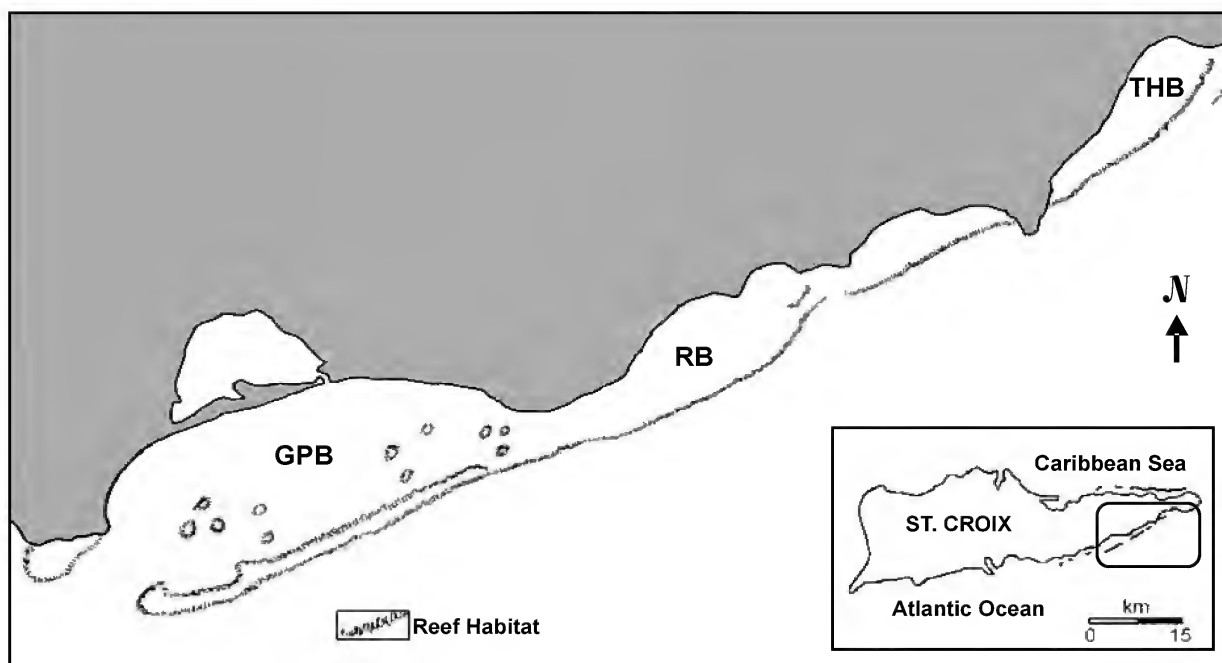


Figure 1. Location of the southeastern backreef lagoon of St. Croix, USVI. The 3 embayments studied, Great Pond Bay (GPB), Robin Bay (RB) and Turner Hole Bay (THB) are shown.

MATERIALS AND METHODS

The nearshore nursery habitat types in 3 protected backreef lagoon embayments on St. Croix's southeast coast (Turner Hole Bay, Robin Bay and Great Pond Bay) (Figure 1) were sampled monthly from July 2000 to July 2001. For each bay, a 20 m x 20 m grid pattern was laid over a nautical chart. Grid intersecting points were labeled with consecutive numbers and were the basis for selecting transect starting points for each embayment. The number of starting points surveyed (10 in each of the 3 embayments) was based on a preliminary fish census (Rogers et al. 1994), and each starting point was selected randomly each month. At each of the 10 starting points, a single 50 m transect line (marked at 1 cm intervals) was laid out on a compass bearing randomly selected for each transect. At each starting point, one weighted end of the 50 m transect line tape was dropped and was laid by a diver in the direction of the compass bearing. On each transect, 100 m² were surveyed visually for fish, with 2 parallel 1 m x 50 m belt transects surveyed by 2 divers swimming on opposite sides of the transect line.

At each transect site, a fish census and a benthic survey was done. Each diver recorded fish species and size class of individuals for each species and size class. Fish size classes were characterized as < 5 cm, 5–10 cm, and > 10 cm in total length (TL). For most species, juveniles ≤ 5 cm were recorded as recruits. For smaller species,

such as wrasses, grunts, and damselfishes, juveniles ≤ 3 cm were considered as recruits. Larger individuals in size classes 5–10 cm and > 10 cm were considered as sub-adults. To minimize the potential bias of counting the same individual twice along the belt transect, divers conferred with each other using hand signals to make sure fish were counted only once (Eberhardt 1978), and divers were trained to maintain constant swimming speed along the transect, and not to count fish that entered the census area after the visual census had started (Samoylis and Carlos 2000).

For the benthic survey, each diver recorded the dominant habitat type at the beginning and end of changes in habitat type (to the nearest cm) under the transect line. Five benthic habitat types were identified:

Patch reef: isolated, high calcareous structure (not part of the contiguous reef) with a vertical profile that often, but not always, contained live coral cover.

Rubble: low-relief calcareous structure composed primarily of dead/dying coral fragments that were not attached to the habitat type.

Sand: areas of open sand with little (<10% cover) or no plants or coralline material, mostly unvegetated.

Algal plain: sandy bottom dominated by (>60% cover) *Dictyota* spp., *Halimeda* spp., *Penicillus* spp., *Acanthophora* spp., and/or *Udotea* spp., which may have include sparse stands of *Syringodium filiforme* and *Thalassia testudinum*.

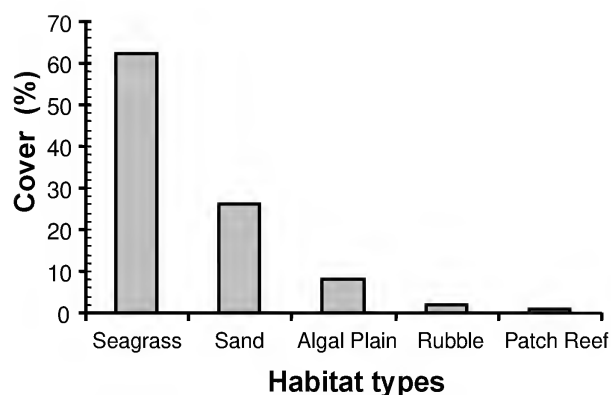


Figure 2. Plot of the total percent of habitat cover found on southeastern barrier reef lagoons in St Croix when all bays were pooled. Number of samples per habitat $N = 24$. Total area surveyed = 70,000 m²

Seagrass: monospecific or nearly monospecific stands of, with varying densities of *S. filiforme*.

Percent cover of each habitat type was estimated from linear coverage along belt transects. The proportional composition of each habitat type covered in each belt transect was estimated by measuring the length of line overlying each habitat type and dividing it by the total length of the transect.

Prior to conducting data analyses, fish density estimates from both divers were checked for independence with a Pearson product-moment correlation coefficient. This was used to test for independence between the paired diver observations (Zar 1984). If uncorrelated, the paired transects could be used as potentially independent samples. We considered $r < 0.50$ to indicate independence. Correlation between paired divers was low ($r = 0.43$, $P = 0.343$, $n = 330$), and we interpreted the data generated from the 2 divers as separate and independent census data sets.

Data were standardized by month by pooling belt transects of all 3 embayments by habitat type. This allowed for equal sample size ($N = 24$) for the one year study. Monthly data were further pooled into winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November) seasons. The seasonal grouping was based on previous temperature measurements done by the USVI Division Fish and Wildlife.

Normality of the number of fish per transect, number of species per transect, size class distribution, and fish density of the most abundant species were verified with the Kolmogorov-Lilliefors Normality test (Zar 1984). Since the estimates failed the normality test even after $\log_{10}(x + 1)$ or square root transformation, non-parametric statistics were used to analyze the data. Overall fish density, species richness, density of the most abundant

species recorded on transects within habitat type, density of economically important species among habitat types and size classes were examined with two-way ANOVA on ranks (Sokal and Rohlf 1981) unless specified. If the overall F-value was significant, Tukey's pair-wise multiple comparison procedure was used to separate mean values. Finally, fish density delineated by habitat type, season and bay were analyzed using the Bray-Curtis similarity measure (Krebs 1999) and clustered using the average linkage method with the PRIMER software package (Plymouth Marine Laboratories, UK).

RESULTS

Species composition among habitat types

Seventy-one fish species were recorded within the St. Croix southeastern backreef lagoonal system. The estimated percent cover of backreef lagoon habitat types pooled by bay was dominated by seagrass and sand, whereas patch-reef and rubble covered the least area of the bottom (Figure 2). Species richness was highest on patch reef (54), followed by rubble (41) and seagrass beds (39) habitats (Table 1), and lowest on algal beds (28) and sandy habitats (10). Thirty-five species occurred over both patch reef and rubble habitats, while the overlap in species between seagrass and the other habitat types was low (Table 1). The most abundant taxa per habitat type were:

Patch reef: *Thalassoma bifasciatum*, *Haemulon flavolineatum*, *Halichoeres bivittatus*, *Acanthurus chirurgus*, and newly settled grunts (*Haemulon* spp.), which all together made up 56% of the total number of fishes recorded from the patch reef habitats.

Rubble: newly settled grunts (*Haemulon* spp.), *H. bivittatus*, *A. chirurgus*, *S. leucostictus* and *T. bifasciatum*, which together made up 76% of the total number of individuals at this habitat type.

Seagrass: newly settled grunts (*Haemulon* spp.), *Sparisoma radians*, *H. bivittatus*, *H. flavolineatum*, and *A. chirurgus*. Those species comprised 90.0% of the total fishes recorded in the seagrass beds.

Algal plain: newly settled grunts (*Haemulon* spp.), *H. bivittatus*, *H. flavolineatum*, *S. radians*, and *A. chirurgus*, which made up 96% of the total number of individuals.

Sand: newly settled grunts (*Haemulon* spp.), *Xyrichtys martinicensis*, *Caranx ruber*, *H. bivittatus*, and *Coryphopterus glaucofraenum*. Those species comprised 98.0% of the fishes recorded in sandy habitats.

Variation in species richness

Species richness differed significantly among habitat types (ANOVA, $P < 0.001$, $df = 4, 20$) but not among sea-

TABLE 1

Fish species abundance on nearshore habitat types in a tropical lagoon in southeastern coast of St. Croix, USVI.

Species	Patch Reef	Rubble	Seagrass	Algal Plain	Sand	Total
<i>Haemulon</i> spp.	337	646	2599	3824	256	7662
<i>Halichoeres bivittatus</i>	406	318	615	241	27	1607
<i>Sparisoma radians</i>	39	71	758	53	0	921
<i>Haemulon flavolineatum</i>	446	59	248	156	0	909
<i>Acanthurus chirurgus</i>	383	134	139	6	1	663
<i>Thalassoma bifasciatum</i>	464	117	21	0	0	602
<i>Stegastes leucostictus</i>	349	144	31	5	0	529
<i>Acanthurus bahianus</i>	210	144	84	36	0	474
<i>Scarus iseri</i>	224	78	21	10	0	333
<i>Stegastes partitus</i>	164	44	3	0	0	211
<i>Xyrichtys martinicensis</i>	11	0	29	25	134	199
<i>Ocyurus chrysurus</i>	31	5	76	28	0	140
<i>Lutjanus mahogoni</i>	25	32	44	17	0	118
<i>Haemulon plumieri</i>	78	2	20	16	0	116
<i>Pseudupeneus maculatus</i>	12	7	71	0	0	90
<i>Cryptotomus roseus</i>	0	0	55	22	4	80
<i>Sparisoma viride</i>	54	22	0	0	0	76
<i>Holocentrus adscensionis</i>	62	8	0	0	0	70
<i>Stegastes adustus</i>	51	8	0	0	0	59
<i>Sphoeroides spengleri</i>	7	4	17	28	0	56
<i>Halichoeres poeyi</i>	4	1	45	5	0	55
<i>Canthigaster rostrata</i>	26	4	8	7	0	45
<i>Acanthurus coeruleus</i>	24	3	14	0	0	41
<i>Caranx ruber</i>	4	0	7	1	28	40
<i>Epinephelus guttatus</i>	32	7	0	0	0	39
<i>Sparisoma chrysopteron</i>	25	9	0	0	0	34
<i>Sparisoma aurofrenatum</i>	32	4	0	0	0	36
<i>Chaetodon striatus</i>	4	11	2	10	0	27
<i>Cephalopholis fulva</i>	17	10	0	0	0	27
<i>Myripristis jacobus</i>	24	0	2	0	0	26
<i>Coryphopterus glaucofraenum</i>	0	17	0	0	9	26
<i>Monacanthus ciliatus</i>	0	1	16	2	0	19
<i>Abudefduf saxatilis</i>	14	1	0	0	0	15
<i>Chromis multilineata</i>	13	2	0	0	0	15
<i>Holocanthus ciliaris</i>	12	0	1	1	0	14
<i>Microspathodon chrysurus</i>	8	4	0	0	0	12
<i>Halichoeres radians</i>	10	2	0	0	0	12
<i>Caranx crysos</i>	0	0	7	4	0	11
<i>Chaetodon capistratus</i>	7	1	2	0	0	10
<i>Pareques acuminatus</i>	10	0	0	0	0	10
<i>Stegastes planifrons</i>	6	4	0	0	0	10
<i>Stegastes variabilis</i>	3	6	0	0	0	9
<i>Xyrichtys splendens</i>	0	0	3	3	1	7
<i>Apogon</i> spp.	2	2	0	2	0	6
<i>Serranus tigrinus</i>	5	1	0	0	0	6
<i>Paralichthys tropicus</i>	0	0	3	1	1	5

TABLE 1 (cont.)

Fish species abundance within nearshore habitat types in a tropical lagoon in southeastern coast of St. Croix, USVI.

Species	Patch Reef	Rubble	Seagrass	Algal Plain	Sand	Total
<i>Balistes vetula</i>	3	2	0	0	0	5
<i>Sphyraena barracuda</i>	0	0	4	0	0	4
<i>Lutjanus synagris</i>	1	0	2	1	0	4
<i>Lactophrys triqueter</i>	0	0	1	1	2	4
<i>Chromis cyanea</i>	3	0	0	0	0	3
<i>Aulostomus maculatus</i>	0	0	2	0	0	2
<i>Calamus bajonado</i>	0	0	2	0	0	2
<i>Lutjanus analis</i>	0	0	2	0	0	2
<i>Bothus lunatus</i>	0	0	1	1	0	2
<i>Cosmocampus elucens</i>	0	0	1	1	0	2
<i>Bodianus rufus</i>	1	1	0	0	0	2
<i>Mulloidichthys martinicus</i>	2	0	0	0	0	2
<i>Pomacanthus paru</i>	2	0	0	0	0	2
<i>Scomberomorus regalis</i>	0	0	1	0	0	1
<i>Sphyraena picudilla</i>	0	0	1	0	0	1
<i>Diodon hystrix</i>	1	0	0	0	0	1
<i>Doratonotus megalepsis</i>	1	0	0	0	0	1
<i>Cephalopholis cruentata</i>	1	0	0	0	0	1
<i>Gerres cinereus</i>	1	0	0	0	0	1
<i>Gobiosoma</i> spp.	1	0	0	0	0	1
<i>Hypoplectrus gummigutta</i>	1	0	0	0	0	1
<i>Hypoplectrus nigricans</i>	1	0	0	0	0	1
<i>Lactophrys</i> spp.	1	0	0	0	0	1
<i>Scorpaena</i> spp.	0	1	0	0	0	1
<i>Synodus foetens</i>	0	1	0	0	0	1

sons (ANOVA, $P = 0.113$, $df = 3, 20$; Figure 3). Post hoc tests showed that species richness in patch reefs and rubble was significantly higher than seagrass, algal beds, and sandy bottom types (Tukey's test, $P < 0.001$). There was no significant interaction between habitat type and season in species richness (ANOVA, $P = 0.082$, $df = 12, 20$; Figure 3).

Variation in fish density

Fish density was significantly different among habitat types (ANOVA, $P < 0.001$, $df = 4, 20$) and seasons (ANOVA, $P < 0.002$, $df = 3, 20$), but there was no interaction between the main effects (ANOVA, $P < 0.360$, $df = 12, 20$; Figure 4). Fish density was significantly highest in patch reefs and rubble relative to seagrass, algal beds and sandy habitat types across all seasons (Tukey's test, $P < 0.001$). Comparisons of fish density pooled by habitat type indicated that fish density observed in summer was statistically higher than in the spring and winter season (Tukey's test, $P < 0.05$).

Similarity of fish faunas among habitat type and season

Fish assemblages recorded from each habitat type tended to cluster together (Figure 5) showing a comparatively high degree of similarity; season appeared to have no effect. Fish assemblages observed over patch reefs and rubble were more similar to each other than to those observed in vegetated and unvegetated habitat types. Unvegetated habitat types clustered together separately from all other habitat types.

Variation in density of economically important species common species by habitat type

Acanthurus chirurgus recruits (< 5 cm) and sub-adults ($5-10$ cm, > 10 cm) were higher in patch reefs and rubble (Figure 6a) than any other habitat types (ANOVA, $P < 0.001$; $df = 4, 8$; Tukey's test, $P < 0.001$). Density of newly settled grunts ($Haemulon$ spp., < 3 cm) were higher on algal plains compared with other habitat types (ANOVA, $P < 0.001$; $df = 4, 8$; Tukey's test, $P < 0.009$;

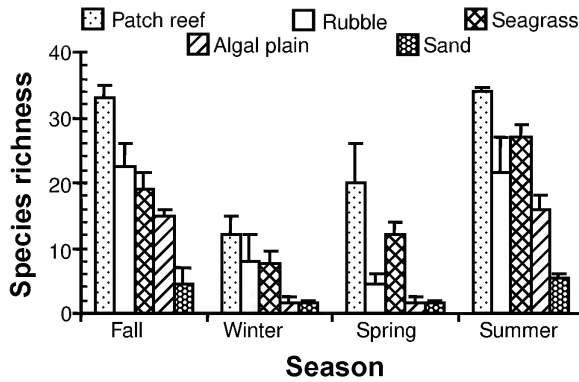


Figure 3. Plot of the mean (s) species richness by habitat type observed during different seasons. s = standard deviation.

Figure 6b). *Scarus iseri* recruits/m² (< 5 cm) were more dominant in patch reefs (Figure 6c), than juveniles (5–10 cm) and sub-adults (> 10 cm)/m² (ANOVA, $P < 0.01$; $df = 4, 8$; Tukey's test, $P < 0.001$). *Ocyurus chrysurus* recruits (< 5 cm)/m² were highest on algal plains and seagrass while larger individuals (> 10 cm) were most abundant on patch reefs (ANOVA, $P < 0.01$; $df = 4, 8$; Tukey's test, $P < 0.02$; Figure 6d). Density (ind/m²) of size class > 5 cm was almost exclusively found in patch reefs for *Haemulon plumieri* (ANOVA, $P < 0.001$, $df = 4, 8$; Tukey's test, $P < 0.003$; Figure 6e) and *H. flavolineatum* (ANOVA, $P < 0.001$, $df = 4, 8$; Tukey's test, $P < 0.002$; Figure 6f). There were no significant interaction terms among habitat type and size class for fish density for all species studied (ANOVA, $P < 0.05$, $df = 8, 20$).

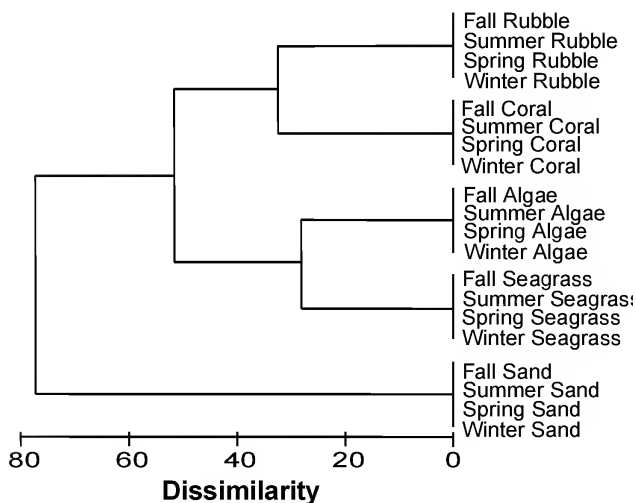


Figure 5. Cluster analysis of fish density by habitat type and season based on visual census using the Bray-Curtis similarity metric and average linkage clustering techniques.

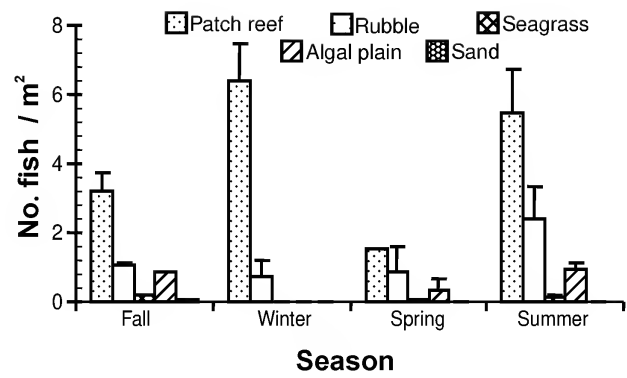


Figure 4. Plot of the mean (s) fish density by habitat type observed during different seasons. s = standard deviation.

Occurrence and density of recruits and non-recruits of common fish species

Recruit density of *H. bivittatus* (ind/m²) was highest in patch reef habitat in summer relative to other habitat types (ANOVA, $df = 4, 20$, $P < 0.001$; Tukey's test, $P < 0.001$; Figure 7a). *Haemulon bivittatus* sub-adults (5–10 cm, > 10 cm) showed significant seasonal differences in density (ind/m²) (ANOVA, $P < 0.004$, $df = 3, 20$; Figure 7b), with the highest mean density being recorded in winter over patch reefs for both size classes (Tukey's test, $df = 4$, $P < 0.001$; Figure 7c). There were no significant interaction terms between habitat type and season for *H. bivittatus* recruits (ANOVA, $P = < 0.686$, $df = 12, 20$) and *H. bivittatus* sub-adults (ANOVA, $P < 0.902$, $df = 12, 20$). A higher density (ind/m²) of newly settled grunts (*Haemulon* spp.) was observed over algal beds during summer and fall seasons (ANOVA, $P < 0.01$; $df = 4, 20$; Tukey's test, $P < 0.009$; Figure 7d). No significant interaction terms between habitat type and season were found for newly settled grunts *Haemulon* spp. density (ANOVA, $P < 0.578$, $df = 12, 20$).

Non-recruit grunt (*Haemulon* spp) density (ind/m²) (5–10 cm) was significantly highest in spring (ANOVA, $P < 0.004$, $df = 4, 20$; Tukey's test, $P < 0.01$; Figure 7e) over patch reef habitats, whereas the density (ind/m²) of grunt >10 cm in patch reefs were highest during summer (Figure 7f). There were no significant interaction terms between habitat type and season in non-recruit *Haemulon* spp. density (ANOVA, $P < 0.563$, $df = 12, 20$).

DISCUSSION

Differences in species richness and fish density

The nearshore environment within St. Croix's south-east bank barrier reef lagoon exhibited distinct patterns in the distribution of fish assemblages among seagrass, algal plains, patch reefs, rubble, and sandy habitat types. The

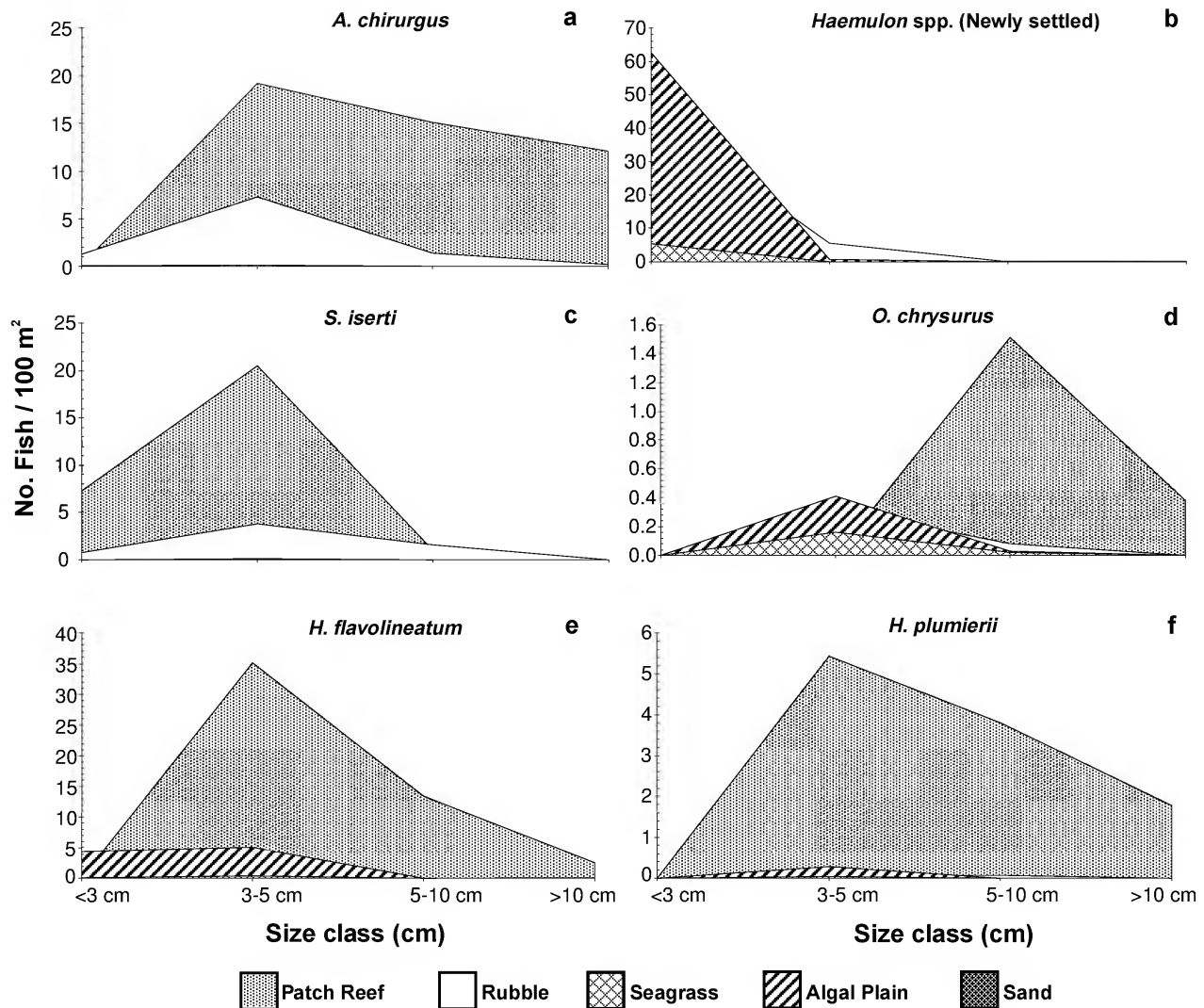


Figure 6. Plot of density of economically important species by size class and habitat types: 6a) *A. chirurgus*, 6b) *O. chrysurus*, 6c) *Haemulon* spp., 6d) *S. iserti*, 6e) *H. flavolineatum*, 6f) *H. plumierii*.

seagrass and algal plain were dominated by small resident species, such as *Halichoeres* spp. and *S. radians*, and by juveniles of non-resident species like *Haemulon* spp. and *O. chrysurus*. Rubble and patch reefs harbored higher species richness and were mostly dominated by small juvenile damselfishes, parrotfishes, grunts, and doctorfishes. The highest species richness occurred over patch reefs and rubble, than over vegetated habitat type types (seagrass, algal plains) and unvegetated sandy habitat types during all 4 seasons. Fish densities were also higher in patch reefs and rubble than over seagrass, algal plains, and sandy bottoms.

Fish assemblages in physically 'structured environments' (patch reef and rubble) tend to be more similar to each other than to those in vegetated (seagrass/algal beds) and unvegetated habitat types (sand) (Nagelkerken et al. 2000, Adams and Ebersole 2002). The cluster analysis

based on our data confirms this pattern, illustrating that fish assemblages from patch reef, and rubble habitat types were more similar to each other, but different from assemblages associated with seagrass, algal plain, and sandy habitat types, regardless of season. Nagelkerken et al. (2000) and Adams and Ebersole (2002) similarly observed a hierarchy in fish abundance within highly structured habitat types (patch reefs, rubble, cobbler) possessing higher density followed by seagrass and then algal beds, and over unvegetated sand bottom.

Seasonal Distribution

Seasonal changes in species composition and density of fish populations were major characteristics in our near-shore lagoonal habitat types. Peak density of total fishes occurred during summer, with a secondary peak in fall and the lowest density of total fishes in winter. Although

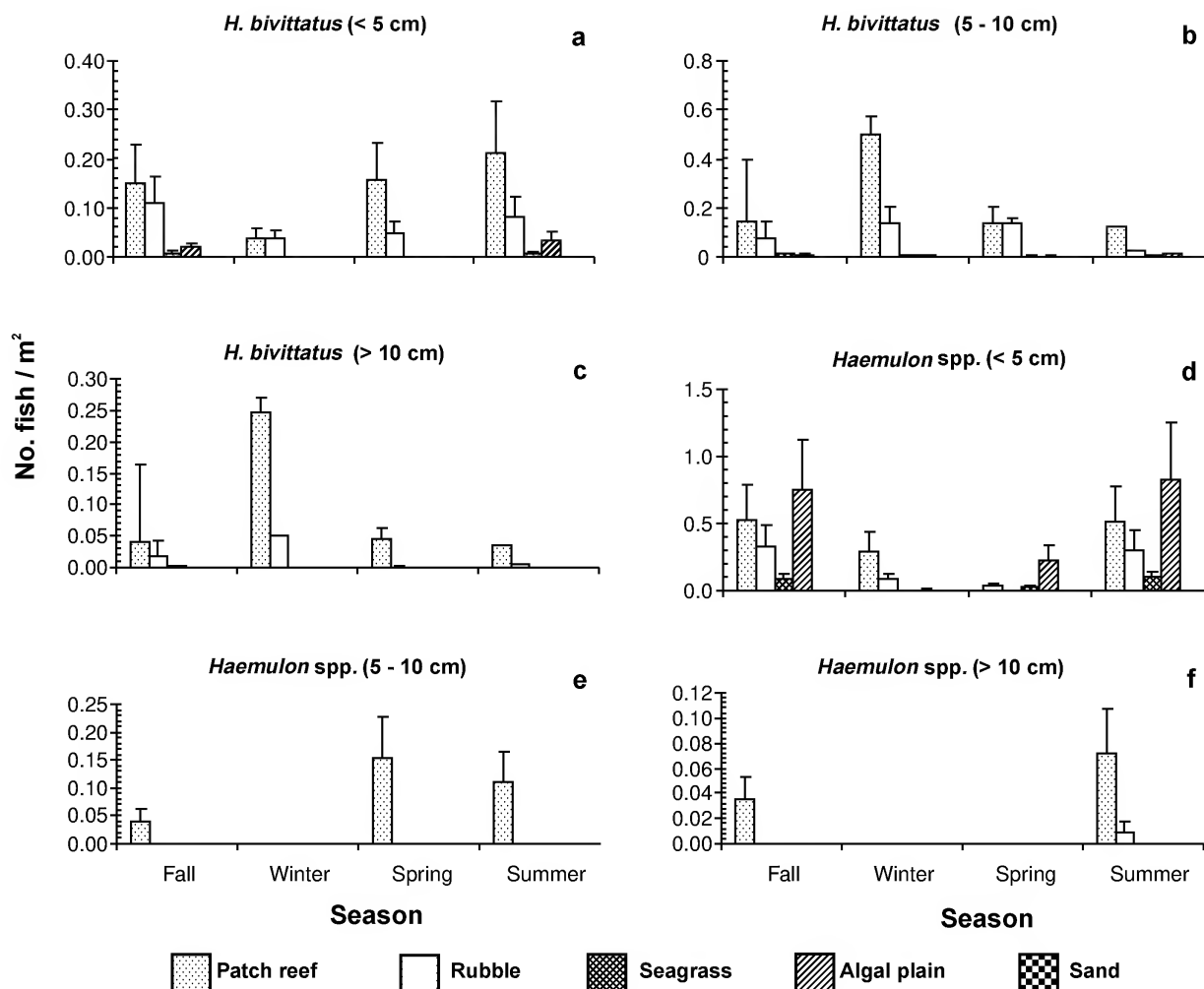


Figure 7. Plot of seasonal occurrence of common species by habitat type: 7a–c) *H. bivittatus*; 7d–f) *Haemulon* spp.; < 5 cm, 5–10 cm, > 10 cm, respectively.

recruits were mainly abundant in the latter half of the summer and in the fall, the pattern of habitat type use by settlers and juveniles differed by species and season. For example, 50% of all recruits occurred in late summer whereas 42% occurred in Fall and 8% in the rest of the year. Tropical fish assemblages have shown seasonal fluctuation characterized both by a higher species richness and by a higher abundance of fishes during the summer and fall, which is influenced by recruitment of juveniles, the increase of food availability, and spawning patterns (Ogden and Gladfelter 1983, Baelde 1990). Considering that much of the research of settling and juvenile fishes in the Caribbean has taken place during the summer, future research should focus on the relative mechanism of transport processes throughout the year.

Habitat type distribution

Distinct patterns of species among habitat types were observed at St. Croix's southeastern barrier reef lagoon

with some species being found exclusively or predominantly in one of the 5 habitat types. The scarid, *C. roseus*, and the labrid, *H. poeii*, for example, were more associated with seagrass, whereas other labrids such as *T. bifasciatum* and *H. radians*, the scarids *S. aurofrenatum*, *S. iseri*, and *S. viride*, and the squirrelfishes *H. adensionis* and *M. jacobus* were found predominantly over patch reefs. Fish species found predominantly over bare sand were *X. martinicensis* and *C. glaucopraenum*. In contrast, *H. bivittatus*, *S. radians*, newly settled grunts *Haemulon* spp., *H. flavolineatum*, *H. plumieri*, the lutjanids *O. chrysurus* and *L. mahogoni*, and the acanthurids *A. chirurgus* and *A. bahianus* were commonly associated with more than one habitat type. The differences in fish size distributions among habitat types suggested different ontogenic distribution patterns by species. For example, many recruits of economically important species (e.g., *S. iseri*, *A. chirurgus*) were on patch reefs and rubble whereas recruits of newly settled *Haemulon* spp. and *O. chrysurus* were mostly in

seagrass beds and algal plains. Density of larger (> 10 cm) fish (e.g., *H. plumierii*, *S. iseri*, *H. flavolineatum*, and *O. chrysurus*) were low in patch reefs and seagrass beds, however. These results reflect the temporary and successive use of seagrass and patch reef habitats by juveniles of various species that move elsewhere as they grow, as it is the case for *O. chrysurus*, and *S. iseri* (Clifton 1991, Tolimieri 1998, Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2002). Changes in habitat type use might also be expected to coincide with size-related changes in individual fitness or physiological requirements (Appeldoorn et al. 1997, Lindeman et al. 1998), or ontogenetic changes in diet, mortality, and/or competitive interactions (Shulman and Ogden 1987, Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2002). For example, some snappers, grunts, and parrotfishes progressively change habitat type with size (Appeldoorn et al. 1997, Lindeman et al. 1998, Adams and Ebersole 2002). *Ocyurus chrysurus*, *H. flavolineatum*, and *H. plumierii* settle onto seagrass beds and algal plains and migrate to nearby reefs at larger sizes (Shulman and Ogden 1987, Appeldoorn et al. 1997, Lindeman et al. 1998). Distribution of *S. iseri* appears to be determined by habitat-based distribution of primary food sources (Clifton 1991, Tolimieri 1998). As their foraging efficiency and home range increases ontogenetically, these nursery areas no longer provide adequate shelter and food sources; thus, the species migrate to deeper habitat like fore-reef and mid-shelf reef to meet their ecological requirements (Clifton 1991, Tolimieri 1998).

Our study suggests that nursery habitats are not limited to seagrass and mangrove systems, but include other nearshore habitats like patch reefs, rubble areas, and algal plains. Patch reefs and rubble habitats had the highest density of fish recruits; however, total counts of fish recruits were higher on seagrass beds and algal plains because of the areal coverage of these latter habitat types in the bays surveyed (Figure 2). In the Caribbean, recent studies of nearshore fish assemblages suggest that patch reefs and rubble areas appear to be important shelter sites for juvenile fishes in mangrove and seagrass dominated lagoons (Risk 1997, Nagelkerken et al. 2000, Adams and Ebersole 2002). For example in Curaçao, shallow-water coral reefs were utilized more by *H. chrysargyreum*, *L. mahogoni*, *A. bahianus*, and *A. saxatilis* as nursery areas than seagrass and mangrove lagoons (Nagelkerken et al. 2000). In southwestern Puerto Rico, *H. flavolineatum*, *O. chrysurus*, and *H. plumierii* showed greater preference for shallow coral reefs as nursery areas than mangrove and seagrass (Murphy 2001). Finally, similar patterns of habitat use were noted for *H. flavolineatum*, *A. bahianus*, and *A. chirurgus* as they were not strictly dependant on

mangroves and seagrass as nurseries but used alternative nursery areas like shallow coral reefs and rubble areas in St Croix (Risk 1997, Adams and Ebersole 2002).

However, to evaluate the role of nearshore habitat types as fish nursery, more studies should be done focusing in understanding how these habitat types may provide a nursery function role to reef fishes. During a study of seagrass and mangrove fishes in Belize, Chittaro et al. (2005) found that based on density, assemblage composition, and relative rates of predation, not all mangrove and seagrass beds appeared to offer nursery function. Their study highlighted the need to avoid generalizations about mangroves and seagrass having nursery related functions, if estimates of density are the only method to confirm nursery potential. Additionally, in the Indo-Pacific, the nursery value of mangroves and seagrass have been questioned as juvenile fishes did not show evidence of using mangroves as shelter (Thollot, 1992, Huxham et al. 2004). Therefore, many factors like density, survival, growth, and movement among habitat types have to be examined simultaneously in order to support a particular habitat type as being a nursery (Beck et al. 2001).

Implications for management

Knowledge of habitat type use patterns by different fish life stages along a cross-shelf gradient is needed to understand the importance of nearshore habitats as nursery areas and presumable ontogenetic shifts in habitat type requirements. Based on these data, it would then be possible to infer connectivity of reef fish migrating among habitat types from inshore to offshore during post-settlement ontogeny (Appeldoorn et al. 1997, Lindeman et al. 1998, Nagelkerken et al. 2000). Determination of nursery value of nearshore habitats and ontogenetic shifts in fish habitat type use (Appeldoorn et al. 1997, Lindeman et al. 1998, Cocheret de la Morinière et al. 2002) would facilitate fisheries conservation and coastal zone management plans. For example, designing marine protected areas (MPAs) and improving the efficacy of the proposed MPAs in areas adjacent to the St Croix East End Marine Park.

As our study suggests, there is increasing evidence that many reef fish are dependent on nearshore systems that comprise a mosaic of habitat types including not only coral habitat structure but also a mixture of seagrass, algal plains, and rubble. Each of these habitat types contains unique biotic communities that vary differently depending on the scale at which individual or community level processes are observed. Strong linkages exist between fish and habitat and successful implementation of marine reserves requires knowledge of location, distribution, and extent of habitat types necessary for successful recruit-

ment, growth, feeding, and reproduction. To measure the efficacy of a marine reserve to enhance fish abundance, it is critical to develop a baseline against which future estimates can be compared. The results found in this study provide a foundation upon which an ecosystem approach could be developed. As resource managers address the placement and design of MPA's, information on habitat type use and life-history characteristics of coral reef fishes are required and will become a vital part of the decision-making process. The use of lagoon habitat types as nurseries by reef-associated fishes must be incorporated into any management plan.

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Abundance and Ecological Distribution of the "Sete-Barbas" Shrimp *Xiphopenaeus kroyeri* (Heller, 1862) (Decapoda: Penaeoidea) in Three Bays of the Ubatuba Region, Southeastern Brazil

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ABUNDANCE AND ECOLOGICAL DISTRIBUTION OF THE "SETE-BARBAS" SHRIMP *XIPHOPENAEUS KROYERI* (HELLER, 1862) (DECAPODA: PENAEOIDEA) IN THREE BAYS OF THE UBATUBA REGION, SOUTH-EASTERN BRAZIL

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ABSTRACT The influence of environmental factors on the abundance and spatial-temporal distribution of the shrimp *Xiphopenaeus kroyeri* was investigated in southeastern Brazil over 2 years. Monthly collections were conducted in Mar Virado, Ubatuba and Ubatumirim Bays using a commercial shrimp fishing boat equipped with 2 "double-rig" nets. Each bay was divided into 6 sampling stations, all of which were less than 25 m deep. The spatial distribution of *X. kroyeri* differed among Bays. Highest abundance values were recorded in areas where silt and clay comprised more than 70% of the bottom sediment. Abundance of *X. kroyeri* followed a seasonal trend, being higher during fall and winter, when intrusions of tropical waters are frequent, causing an increase in salinity (>35‰) and temperature (> 21° C). A clear decrease in shrimp abundance followed a decrease in bottom temperature (< 20° C) during spring and summer due to the influence of cold water currents, particularly the South Atlantic Central Water. These results suggest that sediment type, salinity, and temperature are among the most important variables affecting the spatial and seasonal distribution of this species.

INTRODUCTION

The seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862), commonly known in Brazil as "camarão sete-barbas," is widely distributed in the Western Atlantic from Cape Hatteras (North Carolina, USA) through the Caribbean region to southern Brazil (State of Rio Grande do Sul) (D'Incao 1995, Costa et al. 2000, Castro et al. 2005). This species is the second most important fishery resource in southeastern Brazil and is the most heavily exploited benthic shrimp species on the coast of the state of São Paulo (D'Incao et al. 2002, Castro et al. 2005). In addition, *X. kroyeri* plays an important ecological role in maintaining the stability of trophic relationships in benthic communities (Pires 1992, Nakagaki and Negreiros-Fransozo 1998). *Xiphopenaeus kroyeri* has been heavily exploited over the past few decades, at times accounting for 90% of all penaeoid shrimps caught in shallow waters down to 20 m (Costa 2002, Fransozo et al. 2002). During the 1980s and early 1990s, their combined biomass averaged over 10,000 t/yr but declined to less than 5,000 t/yr in the late 1990s (D'Incao et al. 2002).

Studies on *X. kroyeri* to date have focused on aspects of its geographical and bathymetric distributions (Williams 1984, D'Incao 1995, Boschi 2000), faunal surveys along the São Paulo coast (Nakagaki et al. 1995, Costa et al. 2000, 2003), or abundance and diversity patterns within the benthic community (Pires 1992). However, virtually

nothing is known about the ecological distribution of *X. kroyeri* along the Brazilian coast or elsewhere in the Western Atlantic.

An important aspect of the area investigated is its hydrographic structure (Pires 1992). According to Castro-Filho et al. (1987), 3 water masses are present on the marine continental shelf, with different distribution patterns in summer and winter. Coastal Water (CW) has high temperature and low salinity ($T > 20^{\circ}\text{C}$, $S < 36$ psu), Tropical Water (TW) has both high temperature and salinity ($T > 20^{\circ}\text{C}$, $S > 36$ psu), and South Atlantic Central Water (SACW) has both low temperature and salinity ($T < 18^{\circ}\text{C}$, $S < 36$ psu). These water masses interact to modify the temperature, salinity, and food availability during the course of the year.

We analyzed the spatial and temporal distribution patterns of *X. kroyeri* in 3 Bays in the Ubatuba region, São Paulo State, Brazil. Abundance patterns are related to variation in salinity, temperature, depth, sediment composition, and organic-matter content.

MATERIAL AND METHODS

Shrimp were collected monthly from January 1998 to December 1999 in Mar Virado (MV), Ubatuba (UBA), and Ubatumirim (UBM) Bays, located in the Ubatuba region, state of São Paulo. Each bay was classified into 6 stations, which were selected to include the full range

of environmental conditions where *X. kroyeri* is found. These conditions included: their position relative to the bay mouth, depth, and sediment type; the presence of a rocky wall or beach along the bay shore; the inflow of fresh water; and the proximity of offshore water, i.e., open areas with higher salinity. Four of the stations were located at mean depths of 5 (IV), 10 (III), 15 (II) and 20 m (I), and 2 were established adjacent to rocky shores (an exposed and a sheltered shore, stations V (9 m) and VI (6.5 m), respectively) (Figure 1). A shrimp-fishing boat equipped with 2 double-rig nets (mesh size 20 mm and 15 mm in the cod end) was used for trawling. At each station we trawled over a 30-min period, covering 18,000 m².

At each station, salinity and temperature (bottom and surface water), depth, organic matter content (%), and grain size of sediments were measured. The sampling methods and the analysis of environmental factors during the same period have been described by Bertini et al. 2001. Bottom water was sampled using a Nansen bottle. Salinity (psu) was measured with a optic refractometer Atago S/1000 and temperature (°C) using a thermometer attached to the bottle. An ecobathymeter coupled with a GPS was used to record depth (m) at sampling stations. Sediment samples were collected at each station with a Van Veen grab (0.06 m²). In the laboratory, the sediment was oven-dried at 70° C for 72 h. For the analysis of grain size composition, two 50-g sub-samples were treated with 250 ml of a 0.2 N NaOH solution, stirred for 5 min to separate the silt and clay particles, and then rinsed on a 0.063-mm sieve.

Sediments were sieved through 2 mm (gravel); 2.0–1.01 mm (very coarse sand); 1.0–0.51 mm (coarse sand); 0.50–0.26 mm (medium sand); 0.25–0.126 mm (fine sand); and 0.125–0.063 mm (very fine sand); smaller particles were classified as silt-clay. Grain size categories followed the American standard (Wentworth 1922), and fractions were expressed on the phi (Ø) scale, thus accounting for the central tendency of sediment samples, e.g., $-1 = \phi < 0$ (gravel); $0 = \phi < 1$ (coarse sand); $1 = \phi < 2$ (intermediate sand); $2 = \phi < 3$ (fine sand); $3 = \phi < 4$ (very fine sand) and $\phi \geq 4$ (silt + clay) (Tucker 1988). Cumulative particle-size curves were plotted on a computer using the phi scale, with values corresponding to 16th, 50th, and 84th percentiles being used to determine the mean diameter of the sediment using the formula $Md = (\phi_{16} + \phi_{50} + \phi_{84})/3$. Finally, phi was calculated using the formula $\phi = -\log_2 d$, where d = grain diameter (mm) (Tucker 1988).

The organic matter content (%) was obtained by ash-weighing: 3 aliquots of 10 g each per station were placed in porcelain crucibles and burned for 3 h at 500° C, and the samples were then weighed again (see Mantelatto and Fransozo 1999).

The abundances of shrimps were compared among years, bays, stations, and seasons (summer (January–March), autumn (April–June), winter (July–September), and spring (October–December)) of the year using an analysis of variance factorial model (ANOVA, $P < 0.05$). The homoscedasticity (Levene test) and normality assumptions

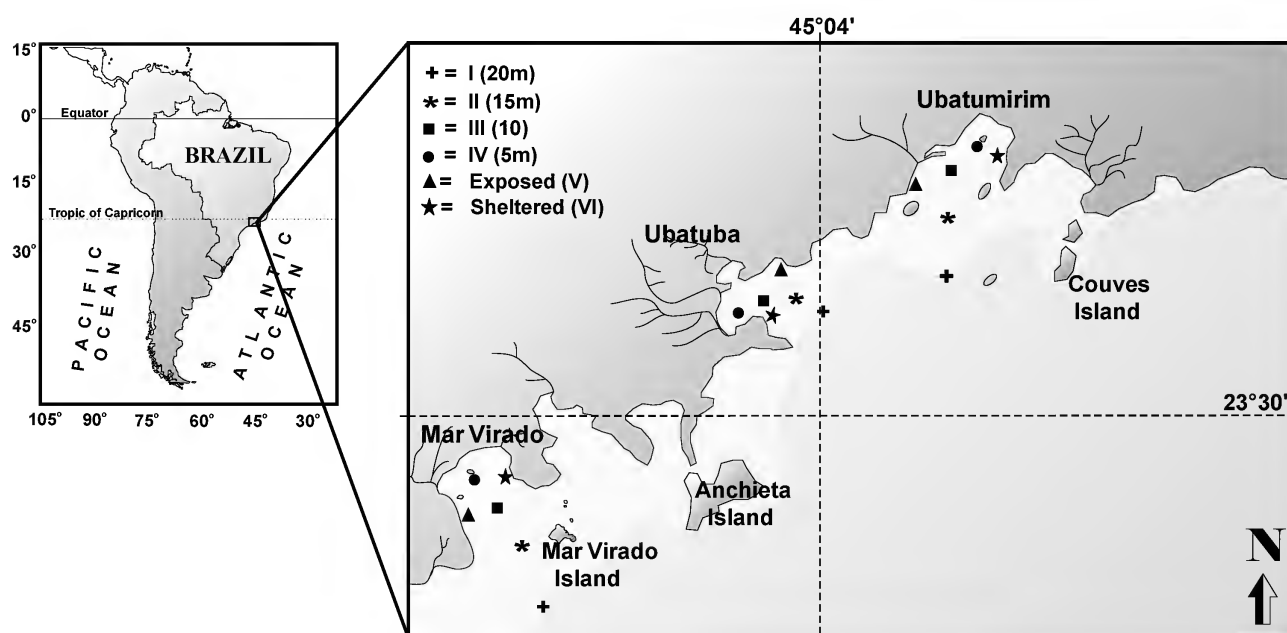


Figure 1. Map of the Ubatuba region with the indication of stations in each bay.

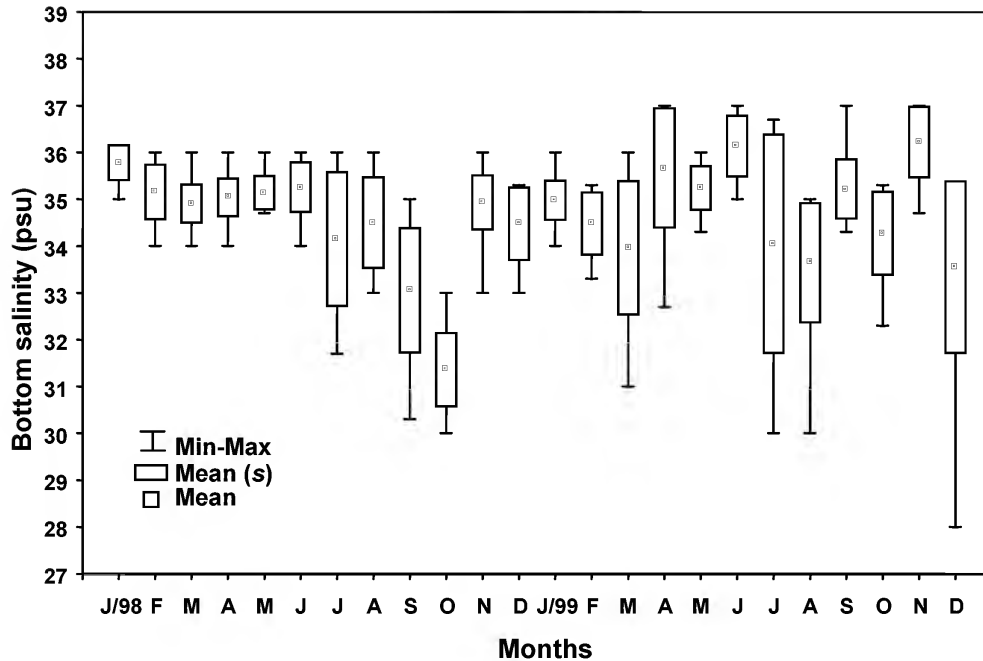


Figure 2. Boxplot showing mean ($\pm s$), maximum and minimum salinity values for each month during 1998 and 1999. s = standard deviation.

were examined and the data were \log_{10} -transformed prior to the analysis (Zar 1999). The influence of environmental factors on the species abundance was evaluated by multiple linear regression and also compared through analysis of variance (ANOVA, $P < 0.05$) (Zar 1999).

RESULTS

Monthly and among-station variations in mean bottom salinities are shown in Figures 2 and 3. In general, highest

salinity values (> 35 psu) were found during the autumn (May and June in 1998 and April–June in 1999), whereas the lowest values occurred during early spring (September and October) in the first year and during winter and spring (except November) during the second year.

Temperature within each season was significantly lower in the second year. Clear temperature differences were found among stations during spring and summer, with stations I–III being cooler than stations IV–VI (Figure 4). Mean temperature values were homogeneous among

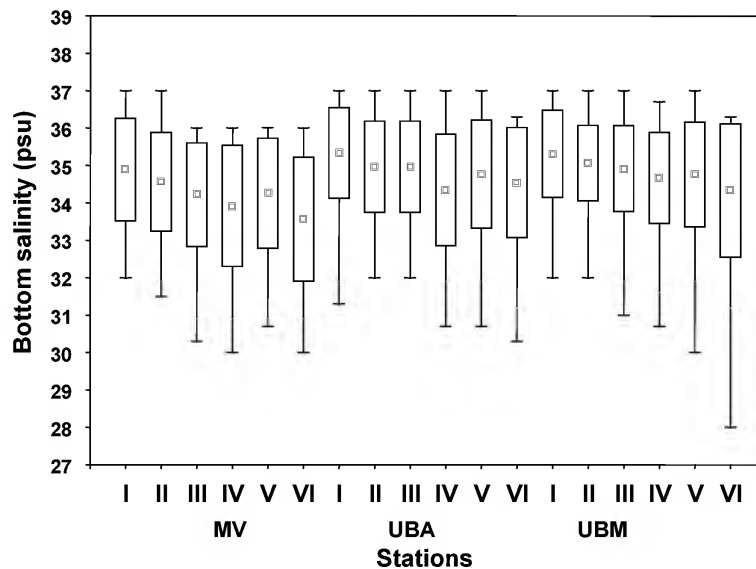


Figure 3. Boxplot showing mean ($\pm s$), maximum and minimum salinity values for each station in the bays during 1998 and 1999. MV, Mar Virado; UBA, Ubatuba; and UBM, Ubatumirim. s = standard deviation.

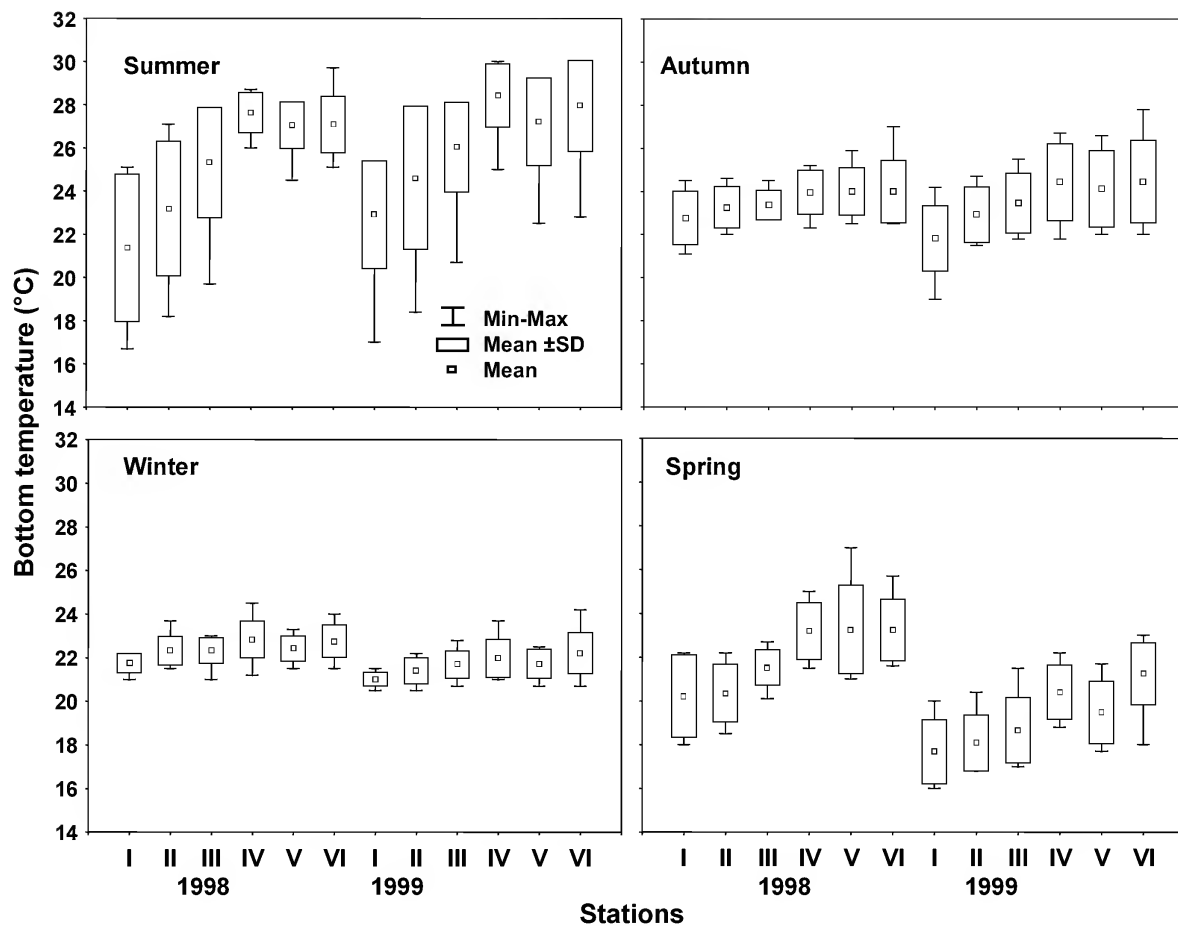


Figure 4. Boxplot showing mean ($\pm s$), maximum and minimum temperature values for each station and season during 1998 and 1999. s = standard deviation.

stations in other seasons. Organic matter contents at each station of each bay are shown in Table 1. Differences in mean organic-matter content levels were found among embayments, with deeper stations located near the bay mouth (I and II) showing the lowest levels.

The amount of mud in the sediments decreased northward, i.e., from Mar Virado Bay to Ubatumirim Bay (Table 1, Figure 5). In Mar Virado Bay, the silt + clay fraction ($\phi > 4$) was the most prevalent at the majority of stations, with values above 70% at stations II through V. A predominance of fine and very fine sand, associated with silt and clay, was observed in Ubatuba, particularly in Ubatumirim Bay (Table 1), except for stations VI in Ubatuba Bay and station I in Ubatumirim Bay.

A total of 563,636 individuals were collected during the present study; 324,861 during the first and 238,775 during the second year. In both years, the abundance of *X. kroyeri* was higher in Mar Virado Bay (248,792), compared to Ubatuba Bay (206,284) and Ubatumirim Bay (108,560). The differences among bay and year were statistically significant ($P < 0.05$, Table 2).

The highest shrimp abundance occurred during fall and winter in 1998 and during fall in 1999 (Figure 6), periods when shrimp abundance was significantly higher than in other seasons ($P < 0.01$). Conversely, lowest abundance occurred during summer and spring, particularly in 1999. The interaction between year and season was also significant (Table 2).

About 82% of all shrimps were caught in shallow areas, i.e., depths < 15 m (Figures 7 and 8, Table 1), except at station VI in Ubatuba Bay. Substantial differences in abundance were found among stations ($P < 0.001$) and between its interactions with bay ($P < 0.001$) and season ($P < 0.05$; see Table 2); no other interactions were observed ($P > 0.05$).

The correlation ($r = 0.49$) between abiotic factors and variation in shrimp abundance indicated that more individuals were collected in conditions of medium bottom temperature (22–24° C) and high salinity (36–38 psu). With respect to the substrate, shrimp abundance increased in areas with high organic matter content and high percentage of silt and clay (high ϕ values). Also, in spring and

TABLE 1

Mean values of sediment parameters (diameter = phi; mud content = % silt + clay; organic matter content = o.m.), and number of individuals (*N*) for each station in each sampled bay from 1998 to 1999.

STA	Mar Virado Bay				Ubatuba Bay				Ubatumirim Bay			
	phi (ϕ)	mud (%)	o.m. (%)	<i>N</i>	phi (ϕ)	mud (%)	o.m. (%)	<i>N</i>	phi (ϕ)	mud (%)	o.m. (%)	<i>N</i>
I	4.3	46.8	3.0	17,613	3.2	16	3.6	5,657	1.5	2.6	2.1	3,011
II	5.7	75.3	4.6	47,632	4.0	21.2	4.2	19,240	3.8	23.9	3.4	10,162
III	6.2	88.3	5.4	42,946	5.3	61.9	8.0	52,096	4.4	35.7	5.2	43,357
IV	5.9	81.2	5.6	52,944	5.7	76.3	5.7	49,074	4.9	49.6	4.2	15,607
V	5.8	79.7	4.2	50,753	4.8	47.3	7.5	79,481	4.0	22.2	2.4	16,788
VI	5.4	64.4	4.4	36,904	3.6	36.8	6.1	736	4.4	33.4	4.2	19,635
Total				248,792				206,284				108,560

summer the number of individuals decreased at stations with depths over 20 m (Figure 8). The same periods and stations had low temperatures (Figure 4). In other seasons, particularly autumn, the spatial distribution of *X. kroyeri* was more homogeneous.

There was a good fit of the multiple regression analysis using significant ($P < 0.05$) environmental variables and the abundance of *X. kroyeri* ($r = 0.49$, $P < 0.001$, $F = 69.95$, $N = 432$), which can be expressed as:

$$A = -176.447 + 18.432s + 42.347 \phi$$

where: *A* = abundance; *s* = bottom salinity (partial correlation = 0.11, $P < 0.05$); ϕ = phi (partial correlation = 0.49, $P < 0.05$).

The abiotic factors such as sediment (phi) and salinity were positively correlated with the number of collected

individuals. No significant relationship was observed between bottom temperature or water depth and abundance ($P > 0.05$).

DISCUSSION

The most important variables affecting the spatial and seasonal distribution of *X. kroyeri* in this study were sediment type, salinity, and temperature. This was exemplified by the high abundance of the species in areas characterized by muddy substrates, and high salinity and temperature.

The northern coast of São Paulo state is strongly influenced by 2 water masses: CW and TW. The effects of these water masses are felt most during autumn and winter, when temperature and salinity levels increase to over 21° C

TABLE 2

Results of the analysis of variance (factorial ANOVA) of the number of individuals collected (\log_{10} -transformed) of *Xiphopenaeus kroyeri* by year, bay, or season and station.

Source	df	MS	<i>F</i>	<i>P</i>
Year	1	2.48	4.66	0.03
Bay	2	16.36	30.73	0.00
Station	5	31.15	58.51	0.00
Bay x Station	10	5.71	10.73	0.00
Season	3	16.31	30.63	0.00
Season x Year	3	1.47	2.76	0.04
Season x Station	15	0.93	1.75	0.04

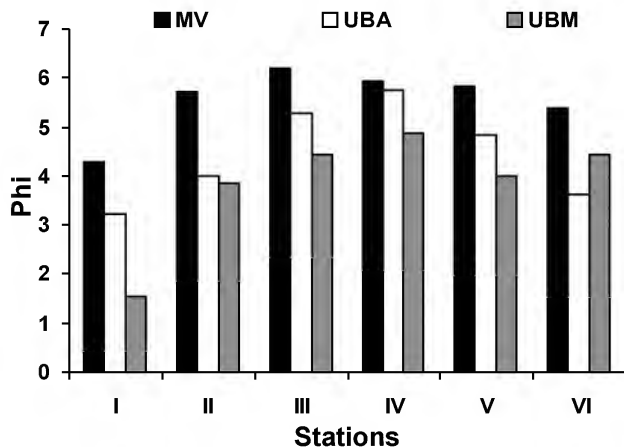


Figure 5. Mean diameter of sediment grains (phi) at each sampled station in the bays studied. MV, Mar Virado; UBA, Ubatuba; UBM, Ubatumirim.

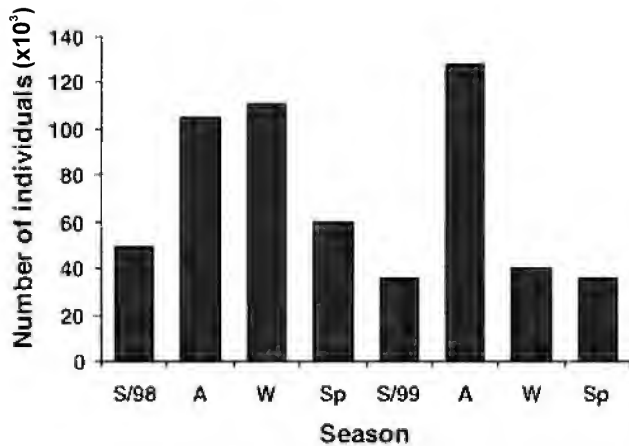


Figure 6. Number of individuals of *X. kroyeri* obtained by season in the sampled Bays during the 2-yr period.

and 35 psu, respectively. Another water mass, the SACW, intrudes throughout late spring and summer causing decreases in temperature ($< 20^{\circ}\text{C}$) and bottom salinity (< 5 psu). The incursion of the TW into the uppermost water layers and the dislocation of the CW toward the ocean during the fall and winter causes vertical mixing and thus eliminates the existing seasonal thermocline causing the SACW to recede towards the offshore region (Castro-Filho et al. 1987, Castilho et al. in press).

In addition to corroborating the scenario described above, our results indicate that fluctuations in the seasonal and bathymetric distribution of *X. kroyeri* were influenced by variation in temperature (summer) and salinity levels caused by these water masses. Therefore, the influence of the SACW in the spring and summer most likely led to a decrease in the number of collected individuals. The retreat of this water mass and the incursion of TW during

autumn and winter considerably increased the abundance of *X. kroyeri*. Similar results were found by Fransozo et al. (2002) for *X. kroyeri* in Fortaleza Bay, by Costa and Fransozo (2004) for *Rimapenaeus constrictus* (Stimpson, 1874), and by Costa et al. (2005a) for *Sicyonia dorsalis* Kingsley, 1878, all in the Ubatuba region. In addition, the number of captured individuals in these studies was smaller in these periods when compared with autumn and winter. Several authors (Rodrigues et al. 1993, Nakagaki and Negreiros-Fransozo 1998, Castro et al. 2005) have hypothesized that individuals of *X. kroyeri* migrate to deeper regions to spawn, given that their main reproductive period occurs during spring and summer. However, even after 3 yr of sampling stations up to 40 m deep in Ubatuba Bay, Costa (2002) and Pinheiro (2004) did not find a single individual of *X. kroyeri* deeper than 25 m. Therefore, one can infer that these shrimp migrate to the northernmost region of southeastern Brazil upon the arrival of the cold water currents. According to Castro-Filho et al. (1987), the SACW reaches its northern limit off the state of Rio de Janeiro, north of which temperatures are markedly higher than off southern Brazil.

There was a marked increase in abundance during winter, even though bottom temperature dropped considerably. This inverse oscillation in abundance caused by variation in temperature during summer and winter may have masked the association between temperature and shrimp abundance, minimizing its impact on the analysis. Nevertheless, our results suggest that temperatures below 21°C may be limiting for this species.

High abundance of *X. kroyeri* were almost invariably associated with high salinity. This finding is similar to that of Castro et al. (2005), who investigated the population structure of this species in Ubatuba Bay, concluding

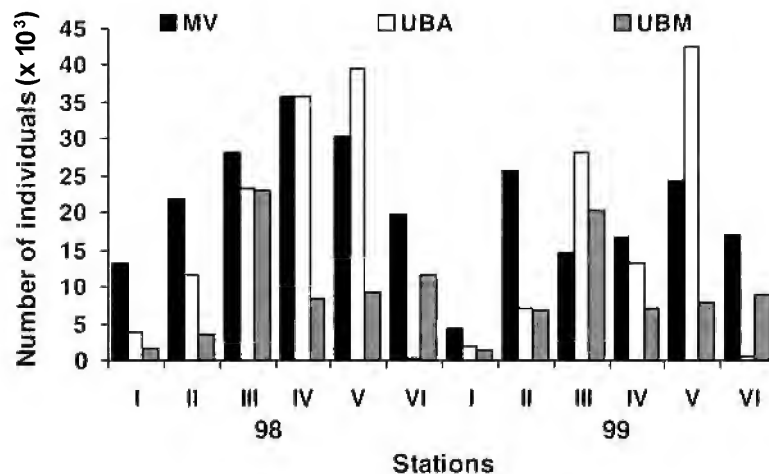


Figure 7. Number of individuals of *X. kroyeri* obtained by station in the sampled bays during the 2-yr period. MV, Mar Virado; UBA, Ubatuba; UBM, Ubatumirim.

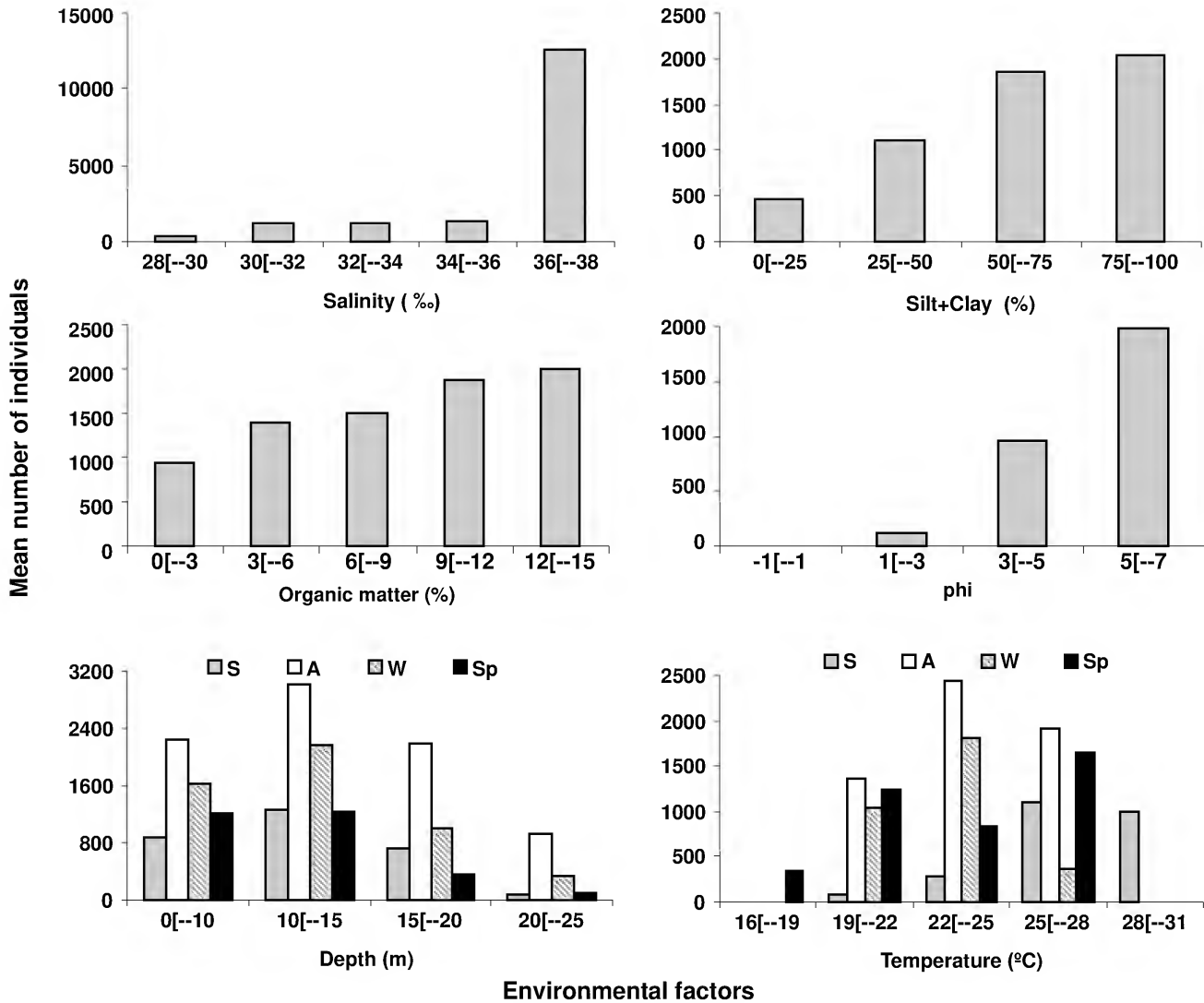


Figure 8. Distribution of the mean number of individuals of *X. kroyeri* in relation to the environmental factors (bottom salinity, silt+clay, organic matter, granulometric classes, depth and bottom temperature). S, summer; A, autumn; W, winter; Sp, spring.

that juveniles are not dependent on estuarine regions and complete their life-cycles in salinities above 30 psu. In contrast, our results contradict other studies that suggest that *X. kroyeri* is euryhaline but only tolerates salinities between 21.2 psu and 36 psu in many parts of its geographical range, such as the coast of Texas, USA (Gunter et al. 1964), the Laguna de Términos, Mexico (Signoret 1974), and the Caribbean coast of Colombia (Cortés and Newmark 1992). These contradictory observations may result from the presence of only small estuaries in the Ubatuba region (Costa and Fransozo 1999).

The abundance of *X. kroyeri* was strongly associated with the mud content of the substrate in each bay, which increased southward from Ubatumirim Bay to Mar Virado Bay. Therefore, the high abundance of *X. kroyeri* in Mar

Virado Bay is probably a result of the high silt and clay content. The increasingly mixed sediments in other embayments, such as at station VI in Ubatuba Bay and station I in Ubatumirim Bay, seem to be avoided by this species.

Given that penaeoid shrimps usually prefer substrates with higher mud and silt content, probably to facilitate their burrowing behavior, this characteristic may affect their distribution (Dall et al. 1990). However, a preference for a given kind of sediment seems to be species specific. In another study at the same site, Costa et al. (2004) found the same spatial distribution in the shrimp *Pleoticus muelleri* (Bate, 1888), and *Artemesia longinaris* Bate, 1888 was found at sites with higher percentages of fine and very fine sands (Fransozo et al. 2004, Costa et al. 2005b). On the other hand, the shrimp *R. constrictus*

showed a stronger preference for much coarser substrates (Costa and Fransozo 2004). According to Penn (1984), preference for a given substrate in the case of penaeoids is associated with their capacity to perform gas exchange when burrowed.

Several authors have suggested that the distribution of penaeoid shrimps is strongly modulated by the texture and organic content of the substrate (Rulifson 1981, Somers 1987, Stoner 1988, Dall et al. 1990, Sanchez 1997). In the present study, the distinctive characteristics of each bay determined to a large extent the differences in the abundance of *X. kroyeri*. However, no correlation was detected between shrimp abundance and the organic content of the substrate.

Even though water depth was not identified as a significant predictor of the abundance of *X. kroyeri* in multiple regression analyses in our study, this result should be interpreted with caution, given that this abiotic factor is usually co-linear with bottom temperature and the type of sediment. Pires (1992) studied the decapod community in the Caraguatatuba region, the southernmost part of the north shore of the state of São Paulo and encountered specimens of *X. kroyeri* in depths between 50 and 60 m. High mud contents were found at these depths compared to other sites farther north. When viewed in the light of our study, these results suggest that the sediment with higher mud content allowed an expansion of their bathymetric distribution and thus might represent an essential factor for the establishment of this species.

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GROWTH PHASES AND DIFFERENTIAL GROWTH BETWEEN SEXES OF *UCA MARACOANI* LATREILLE, 1802–1803 (CRUSTACEA, BRACHYURA, OCYPODIDAE)

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ABSTRACT Among crustacean decapods, fiddler crabs of the genus *Uca* are the most characteristic of the intertidal zones of tropical and subtropical estuaries. The present study determined the growth phases and the beginning of differential growth between the sexes, based on analyses of relative growth of *Uca maracoani*. Collections were made in the Jabaquara mangrove, located in Paraty, Rio de Janeiro, Brazil. Specimens were collected manually during low tide periods. In the laboratory, crabs were sexed and measured. We measured carapace width (CW), carapace length (CL), propodus length (PL; the right one for females and the major one for males), propodus height (PH), abdomen width (AW), and gonopod length (GL; for males). The beginning of differential growth between the sexes could be identified by the allometric technique. Males and females showed 3 distinct growth phases. Differential growth between sexes began when males reached 7 mm and females 9.2 mm CW. The growth pattern among different phases and the beginning of differential growth seemed to maintain a strict relationship with the ontogenetic changes, mainly those related to behavioral and reproductive aspects. This information is important for general biological knowledge of this species, mainly concerning aspects of its growth.

INTRODUCTION

Fiddler crabs of the genus *Uca* Leach, 1814 show a distinct sexual dimorphism. The chelipeds of females are symmetrical and small; both are adapted for catching and passing substrate particles to the mouth appendages. In males, one cheliped is more developed than the other, and is used for interaction with other males and defense of territory; only the smaller cheliped is utilized to scoop a small amount of material from the substrate and transport it to the mouth for feeding (Yamaguchi 1977, Christy and Salmon 1984, Rosenberg 2002), like those of the female.

The study of growth in crabs is facilitated by the hard tegument and the periodic change in the exoskeleton at molting. This makes possible exact measurements and observations of ontogenetic subdivisions in the body size at the beginning of morphological sexual maturity (Huxley and Teissier 1936).

Several aspects of the minor and major chelipeds of fiddler crabs have been studied. These studies have treated the morphological structures (Crane 1975, Yamaguchi 2001), variations in shape (Rosenberg 1997, 2002), sexual differences (Yamaguchi, 2005), handedness (Jones et al. 1982, Williams et al. 1981, Yamaguchi et al. 2001), and growth (Hartnoll 1974, 1978, 1982). The differential growth of the large chelipeds of males, as well as other body parts such as male gonopods and the abdomen of females (Hartnoll 1974, 1978), reveal the transition from juvenile to adult phases (Negreiros-Fransozo et al., 2003). Allometric growth has been studied in several species of

ocypodid crabs, including *Uca tangeri* (see Von Hagen 1987, Colpo et al. 2003), *Uca thayeri* (see Negreiros-Fransozo et al. 2003), *Uca burgersi* (see Benetti and Negreiros-Fransozo 2003), *Uca rapax* (see Castiglioni and Negreiros-Fransozo 2004), *Uca mordax* (see Masunari et al. 2005), and *Uca maracoani* (see Masunari et al. 2005).

We investigated a population of *U. maracoani* Latreille, 1802–1803 from the mud beach of the Jabaquara mangrove at Paraty, Rio de Janeiro, Brazil focusing on the determination of growth phases and the beginnings of differential growth between the sexes, based on relative growth.

MATERIAL AND METHODS

Uca maracoani occurs along coastlines in the Western Atlantic, including the Antilles, Venezuela, and the Guyanas. It is found along nearly the entire coast of Brazil, from the state of Maranhão south to Paraná (Melo 1996).

Sampling was carried out monthly on the mud beach of the Jabaquara mangrove (23°12'10.0"S, 44°43'14.1"W) from January to July 2003. The crabs were removed from their burrows manually during low tide. Each month, a capture effort of 60 min by 2 collectors was employed. The crabs were packed in plastic bags and frozen for about 2 h.

In order to ensure that the smallest classes were also collected, additional sampling was carried out by 2 people for 20 min, utilizing a small spoon. These small crabs were isolated in small containers, labeled, and transported to the laboratory.

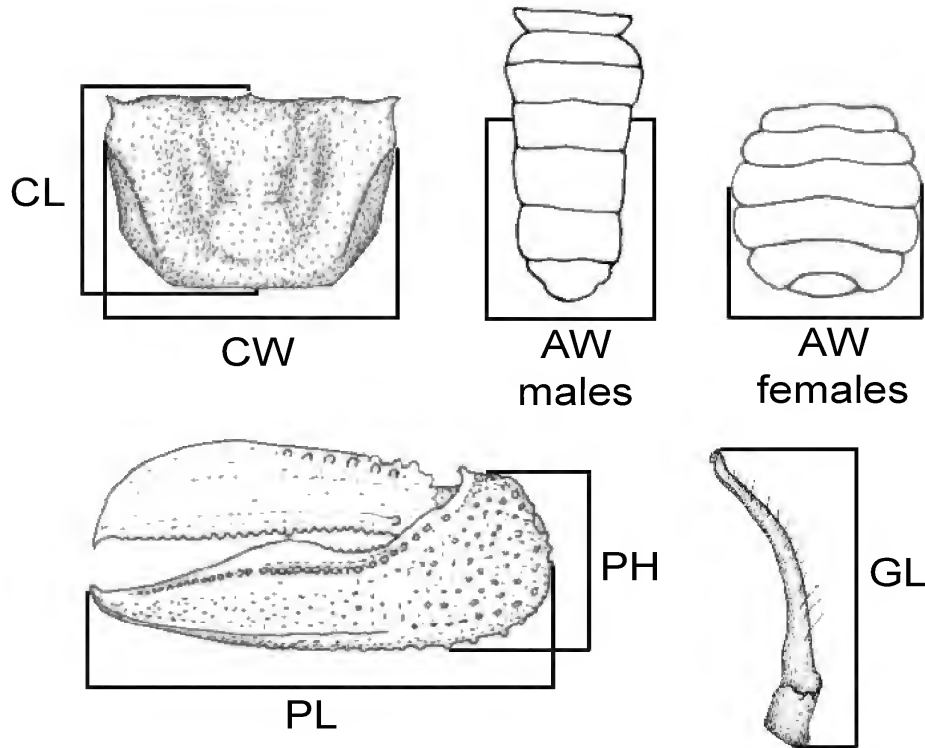


Figure 1. The body parts of *Uca maracoani* measured in this study. (CW = Carapace Width; CL = Carapace Length; AW = Abdomen Width; GL = Gonopod Length; PH = Cheliped Propodus Height; PL = Cheliped Propodus Length.)

In the laboratory, crabs in the intermolt stage were sexed and measured with a digital caliper (0.01 mm), for the following dimensions: carapace width (CW), carapace length (CL), propodus length of the cheliped (PL; right in females and major in males), propodus height of the cheliped (PH), abdomen width (AW) and gonopod length (GL; in males). The measured dimensions are illustrated in Figure 1. Crabs with an imperfect carapace or with body parts in regeneration were not used for analysis.

The smallest individuals, obtained in the additional samplings, were maintained alive in plastic containers with about 20 ml of sea water and fed daily with nauplii of *Artemia* sp. They were monitored daily for the presence of molts until they reached the juvenile stage when they could be identified to species.

The exuvia from each of the first 3 molts only (to minimize the effect of laboratory conditions) were sexed by counting the number of pleopods. Each exuvia was measured under a stereomicroscope for the same body dimensions described above for the adult crabs, except for gonopod length.

Statistical analyses

Relative growth was analyzed based on the allometric technique, for observation of changes in growth of certain body parts in relation to others (Huxley 1950). The data

were plotted in dispersion graphics. Next, the equation of function type $Y = aX^b$ was adjusted to the empirical points and linearized to the form $\log Y = a + b \log X$, where X = the independent variable, using the carapace width (CW); Y = dependent variables, utilizing the other body dimensions; b = allometric constant that expresses the allometric coefficient of body parts in the study. Growth could thus be characterized as positive allometry, when $b > 1$; negative allometry, when $b < 1$; or isometric, when $b = 1$ (Huxley 1950). The " b " value found was tested by Student's t test with significance level $\alpha = 0.05$. To test the similarity of slopes and the intercepts of lines for each phase of development and between sexes, we used a covariance analyses (ANCOVA) ($\alpha = 0.05$) (Zar, 1996).

The programs Mature I and II (Somerton 1980a, b) were used to estimate the size at which males and females changed growth phase, based on the regression analysis of relative growth.

To determine the size at which the differentiation between sexes began, a series of successive covariance analyses was carried out, using intervals of 0.1 mm CW. This proceeded until the point where the lines of growth diverged, or the point at which the males and females attained growth represented by distinct lines ($\alpha = 0.05$).

RESULTS

A total of 563 crabs was collected (253 males and 310 females). Their sizes ranged from 4.9 to 43.7 mm CW (28.5 ± 10.1 mm) for males and from 5.1 to 38.7 mm CW (24.9 ± 7.9) for females. We obtained 92 exuvia from the small individuals raised. The sizes of exuvia ranged from 1.2 to 5.1 mm CW (2.8 ± 0.93); of these, only 7 specimens could be identified as males and 12 as females. The sizes of males ranged from 3.7 to 5.1 mm CW (4.4 ± 0.48) and of females from 3.5 to 5.0 mm CW (4.0 ± 0.51).

The change in growth phases and the beginning of differentiation in growth between the sexes could be expressed by PL vs. CW for males and AW vs. CW for females. The inflexion points of the growth lines related to the change of phases were estimated by means of the Mature I and II programs. Males (< 9.4 ; $9.4 \leq \text{CW} < 21.2$; ≥ 21.2 mm) and females (< 10.3 ; $10.3 \leq \text{CW} < 19.4$; ≥ 19.4 mm) showed 3 distinct growth phases. For females, Mature I indicated the CW50 (19.4 mm) equivalent to the interval of superposition of lines ($16.5 \geq X < 20.9$ mm CW) for juvenile and adult. The regression equations obtained for the growth phases and between sexes were submitted to ANCOVA, which verified that the pattern of growth differed ($P < 0.05$) between sexes and among phases. Thus, we can assume that the lines for different phases (undifferentiated, juvenile, and adult phase) and for sexes (males and females) could be better adjusted to isolated data than in a single line. Exceptions were obtained only for some phases in the relationships CL vs. CW and PH vs. CW (Table 1).

Males and females showed different growth patterns of the carapace. For the relationship CL vs. CW, males showed negative allometry for all phases, whereas the females showed negative allometry only for the juveniles ($b = 0.819$), passing to discrete positive allometric growth in subsequent phases. A slight difference in the shape of the adult male carapace compared with females explained this.

The cheliped relationships PH vs. CW and PL vs. CW showed similar growth patterns. The males, for all age groups, showed positive allometry beginning in the undifferentiated phase ($b = 1.195$; $b = 1.147$ for PL vs. CW and PH vs. CW, respectively), passing to a more positive slope in the later phases ($b = 2.047$ and $b = 1.329$). The females showed less positive allometry compared with the males ($b = 1.056$ for the relationship PL vs. CW), passing to isometry or negative allometry in the case of the juvenile phase and adult females in the relationship PH vs. CW ($b = 0.831$).

For the relation AW vs. CW, sexual dimorphism in growth was very evident. However, in this case, the females showed positive allometry in all age group categories, increasing the slope in the juvenile-phase females ($b = 1.887$). The males showed isometric growth (undifferentiated $b = 0.958$), passing to a positive allometric (juvenile phase $b = 1.174$) and later to a negative allometric growth (adult $b = 0.944$).

Males (smaller than 4 mm CW) were not included in the analyses of the relationship GL vs. CW. The crabs were distributed in 2 age group categories, with different growth patterns ($b = 1.646$ and $b = 0.909$ juvenile phase and adults, respectively).

The onset of differential growth between sexes was at 7 mm CW for males and 9.2 mm CW for females (Figure 2D). Below these points, there was a single line of growth for both sexes ($\alpha = 0.05$).

The patterns of growth found for relationships performed with the data on sex differentiation determined by ANCOVA were the same among the ontogenetic phases, showing positive allometry for the 2 relationships analyzed in both sexes for the undifferentiated and juvenile phases (Table 2).

DISCUSSION

Morphometric data are widely utilized in papers on crustaceans for the study of relative growth (Hartnoll 1974, 1982), especially for detection of changes in the level of allometry, which can be related to certain biological features of the species. Most of the studies on morphological structures in brachyuran crabs have used the dimensions of the carapace, abdomen, and chelipeds as a reference and found distinctive changes in such structures between sexes or growth phases.

In the population studied, *U. maracoani* showed 3 phases of growth. Similar patterns have been reported for other species of the genus: *U. tangeri* studied by von Hagen (1987), and *U. thayeri* studied by Negreiros-Fransozo et al. (2003). Other brachyuran crabs, mainly in the superfamily Majoidea, show similar patterns, although the growth phases are known by different names (Sainte-Marie et al. 1995, Alunno-Bruscia and Sainte-Marie 1998, Sampedro et al. 1999).

The first phase of growth found for *U. maracoani* is represented by morphologically undifferentiated crabs, which only show visible secondary sexual characters in the largest classes. They may not have initiated gonad development; this phase can be called the undifferentiated period.

The first point of the transition is from undifferentiated to a second phase of growth that, probably, is the

TABLE 1

Regression analyses of morphometric data of *Uca maracoani*. Carapace width (CW) was used as the independent variable. CW = Carapace Width; CL = Carapace Length; AW = Abdomen Width; PL = Cheliped Propodus Length; PH = Cheliped Propodus Height; and GL = Gonopod Length. UMF = undifferentiated males and females; UJF = undifferentiated and juvenile female; JAM = juvenile and adult males; JAF = juvenile and adult female; UF = undifferentiated females; JF = juvenile females; AF = adult females; UM = undifferentiated males; JM = juvenile males; AM = adult males; + and – = allometry; 0 = isometry.)

Relationship	Sex	N	Intercep (log)	Slope	r^2	T ($b=1$)	P	Allometry	Results of Mature I and II	
			a	b					F value	Change of phases
CL vs. CW	UMF	196	0.240	0.819	0.981	22.60	0.00	-		
	JAM	255	-0.108	0.967	0.997	29.73	0.00	-		
	JF	56	-0.216	1.060	0.978	2.82	0.00	+		
	AF	136	-0.198	1.043	0.992	5.66	0.00	+		
AW vs. CW	UM	91	-0.626	0.958	0.854	0.97	0.00	0		
	JM	64	-0.818	1.174	0.936	4.47	0.00	+		
	AM	189	-0.495	0.924	0.944	5.00	0.00	-		
	UF	109	-0.680	1.105	0.937	3.74	0.00	+	16.94	10.30 mm
	JF	65	-1.481	1.887	0.927	13.43	0.00	+	72.94	19.30 mm
	AF	221	-0.808	1.377	0.968	22.35	0.00	+		
PL vs. CW	UM	86	-0.500	1.195	0.916	5.00	0.00	+	20.62	9.40 mm
	JM	61	-0.819	1.576	0.969	16.00	0.00	+	140.13	21.20 mm
	AM	180	-1.454	2.047	0.982	50.00	0.00	+		
	UJF	157	-0.453	1.056	0.986	6.60	0.00	+		
	AF	134	-0.377	1.003	0.969	0.00	1.00	0		
PH vs. CW	UM	75	-0.927	1.147	0.855	2.67	0.00	+		
	JM	75	-0.851	1.329	0.967	11.38	0.00	+		
	AM	179	-1.239	1.613	0.976	32.10	0.00	+		
	UF	99	-0.858	0.948	0.923	1.88	0.00	0		
	JAF	190	-0.768	0.831	0.945	12.14	0.00	-		
GL vs. CW	JM	71	-1.177	1.646	0.872	8.53	0.00	+		
	AM	189	-0.269	0.909	0.955	6.43	0.00	-		

beginning of gonad maturation (juvenile phase). In a study on *U. tangeri*, von Hagen (1987) considered the interval between the points of inflexion as a phase of transition or maturation, which extends to the second inflexion point that identifies the transition of individuals to the adult phase.

Adult fiddler crabs can successfully copulate (functional maturity) only when their gonads are mature, i.e., producing gametes, and when they can display specific behaviors, such as the male “waving” display to attract females. Sexual maturation is an extended process that involves gradual ontogenetic changes, rather than a precise moment, such as after the puberty molt (Luppi et al. 2004).

Uca maracoani showed positive allometric growth in the change of phases for sexes and age group categories. The chelipeds of males showed a gradual increase

in allometry among phases, reaching the highest level in adult males. Females showed low, positive allometry in the juvenile phase, considerable positive allometry after the first inflexion point, and then a subsequent decrease after they reached morphological maturity. This growth pattern may reflect the higher energetic investment of females in reproduction during the adult phase. According to Hartnoll (2006), the major energetic needs are for ripening of gonads and formation of associated reproductive products.

Slower growth can also reflect reduced energy intake because of restrictions on feeding. In females, a more general phenomenon is a restriction on feeding during incubation. A further limitation on growth in reproducing females is that they cannot molt while incubating eggs (Hartnoll 2006).

The increase in allometry of chelipeds, in the case of fiddler crab males, just after they reach sexual maturity,

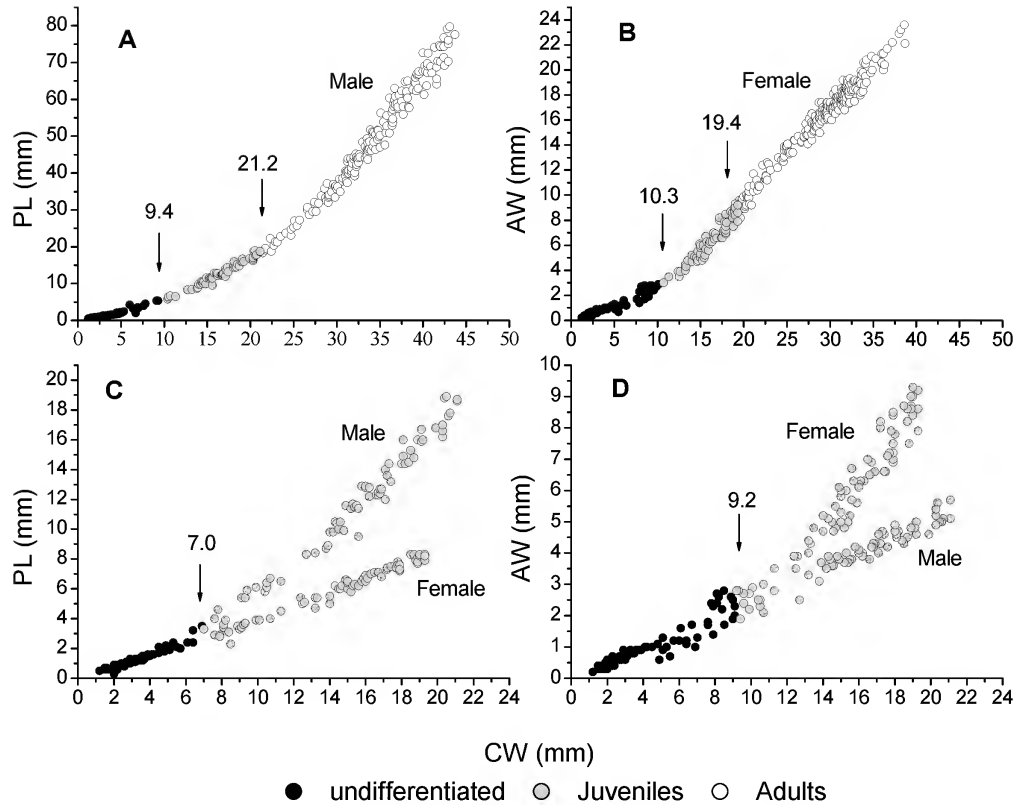


Figure 2. *Uca maracoani*. Dispersion points of relations between the carapace width and the dependent variables. PL = Cheliped Propodus Length; AW = Abdomen Width. A and B are dispersion points related to the changes of growth phases. C and D are dispersion points related to the onset of differential growth between the sexes.

can be very important, because the behavior of cohorts in this genus is predominantly visual. An experimental study with *U. tangeri* by Oliveira and Custódio (1998) found that females spend more time near males with larger claws, in binary choice tests. Large chelipeds are possibly more easily seen by females, increasing the chances that a male's burrow will be visited and he will be chosen for reproduction (Crane 1975, Yamaguchi 1971, Latruffe et al. 1999). In some species, *U. vocans vocans* studied by Salmon (1984) and *U. bebei* studied by Christy (1987), for instance, there is no apparent preference of females for males with larger chelipeds. In such cases, the advantage may be related to the results of fights among males (Crane 1975).

Contests consist of a series of behavioral elements in which the major claw of males plays the principal role (Crane 1975, Salmon and Hyatt 1983, Pratt et al. 2003). In fiddler crabs, the contest duration is expected to reflect the endurance of the weaker of 2 contestants, typically the smaller individual (Hyatt and Salmon 1978, Jennions and Backwell 1996, Pratt et al. 2003). Fighting ability is correlated with carapace width and size of the claw (Hyatt and Salmon 1978), and represents an important feature. Although some contest elements appear dangerous, death or serious injury seldom result (Pratt et al. 2003).

In females, the abdomen widens during growth. This may be related to protection of the gonopores and the mass of eggs during incubation (Hartnoll 1982). The female carapace also widens in relation to that of males, which increases the capacity of the incubatory chamber where the eggs will be carried.

The sexes differed in size at maturity. The larger size of males may reflect strong competition among them, considering that larger males can exert strong influence over smaller males. According to Crane (1975), *U. maracoani* shows a hierarchical behavior, where smaller males avoid combat with the larger, dominant males, leaving the interaction area. In this context, it could be more advantageous for young males to initially invest in growth rather than in reproduction.

Comparing the Paraty population of *U. maracoani* (present study) with the population from Guaratuba studied by Masunari et al. (2005), it is easily realized that there exist significant population differences in relation to growth and morphological sexual maturity. (Table 3) For both sexes, the size at sexual maturity found for the *U. maracoani* population at Jabaquara was greater than for the population at Guaratuba studied by Masunari et al. (2005). This was also seen when the size at differentiation of cheliped (males)

TABLE 2

Regression analyses of morphometric data, based on the growth differentiation between the sexes of *Uca maracoani*. CW = Carapace width; AW = Abdomen Width; PL = Cheliped Propodus Length. UT = undifferentiated males and females; JM = juvenile males; JF = juvenile females; + positive allometry.

Relationship	Sex	N	Intercept (log)		Slope b	r^2	T (b=1)	P	Allometry	Size at differentiation	Results of ANCOVA (P value)
			a	(log)							
AW vs. CW	UT	191	-0.663		1.055	0.89	2.20	0.00	+	9.2 mm	0.06
	JM	65	-0.950		1.281	0.90	13.56	0.00	+		
	JF	70	-1.343		1.773	0.94	15.77	0.00	+		
PL vs. CW	UT	167	-0.458		1.079	0.88	2.63	0.00	+	7.0 mm	0.06
	JM	65	-0.737		1.509	0.97	18.17	0.00	+		
	JF	72	-0.542		1.133	0.95	4.92	0.00	+		

is analyzed. Probably, the large difference between the populations may be responsible for these differences in size at sexual maturity and cheliped differentiation. According to Masunari et al. (2005), the size at differentiation of the cheliped in fiddler crabs apparently is correlated with the maximum size that the species can reach.

The population of *U. maracoani* studied by Masunari et al. (2005) represents, according to Melo (1996), the southern limit of distribution for this species on the Brazilian coast. Consequently, the environmental conditions such as temperature, salinity, food, and size of sediment particles, to which these crabs are exposed, are different from for the population at Jabaquara. This may reflect the differential growth, development, and size of those individuals.

Size variations are common and may reflect the phenotypic plasticity of the organisms or the influence of

environmental factors such as photoperiod, temperature, and food availability (Campbell and Eagles 1983). Such factors can explain the larger CW of specimens of *U. maracoani* from Jabaquara compared with the population at Guaratuba. For a precise determination of which factor or factors are more important for the size difference between these populations, a further, more detailed study would be necessary.

The growth patterns during the different phases, as well as the beginning of differential growth, and morphological sexual maturity seem to maintain a strict relationship with ontogenetic changes, mainly related to behavioral or reproductive aspects and/or environmental factors. This information is important for general biological knowledge of the species, mainly for understanding its growth processes.

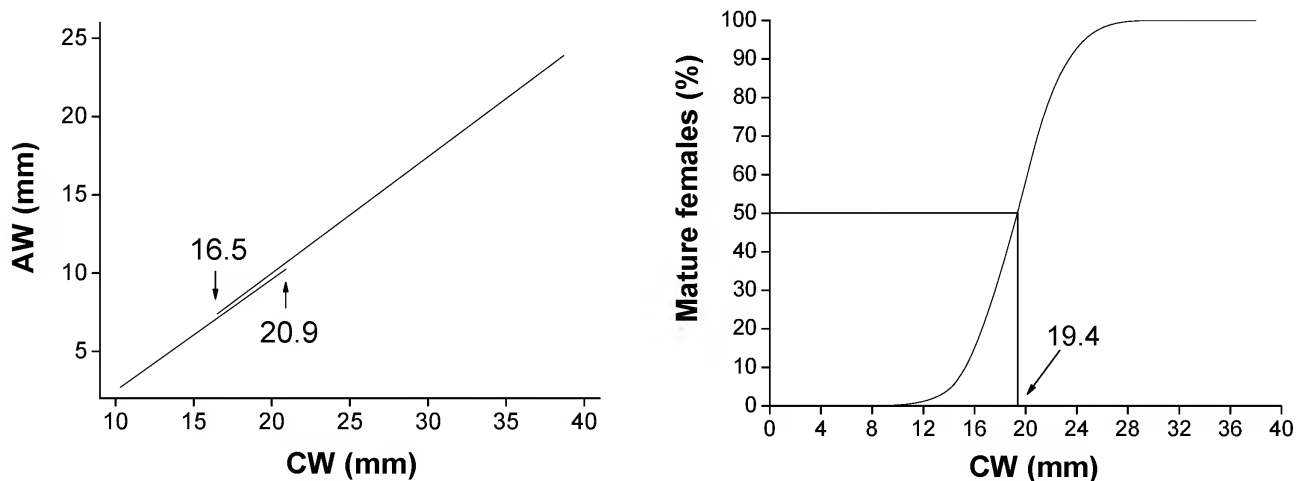


Figure 3. *Uca maracoani*. A – Lines representing the relationships between carapace width (CW) and abdomen width for females. The arrow shows the size at which the puberty molt occurs. B – The logistic equation indicating the size in which 50 % of females are mature.

TABLE 3

Growth features in 2 populations of *Uca maracoani*. Dimensions are in mm. *s* = standard deviation.

Population (reference)	Sex	Maximum size	Mean size $\pm s$	Growth phase	Size at differentiation	Sexual maturity
Paraty, RJ	male	43.7	28.50 \pm 10.1	3	7.0	21.20
(present study)	female	38.7	24.90 \pm 7.9	3	9.2	19.30
Guaratuba, PR	male	34.12	21.53	2	3.27	17.85
(Masunari et al. 2005)	female	29.20	19.13	2	—	11.75

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FIRST RECORD IN HONDURAS OF THE HALFBEAK *HYPORHAMPHUS ROBERTI* HILDEBRANDI, JORDAN AND EVERMAN 1927, (HEMIRAMPHIDAE) COLLECTED IN AN INLAND RESERVOIR

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INTRODUCTION

An inhabitant of tropical America, the Central American halfbeak (*Hyporhamphus roberti hildebrandi*), is one of 2 subspecies of halfbeaks of the subgenus *Hyporhamphus* (Collette 2003, Collette 2004) that belong to the family Hemiramphidae. This family has representatives from the Atlantic, Pacific, and Indian Oceans (Greenfield and Thomerson 1997, Berra 2001, Collette 2004), and nearly all species are marine; however, some Hemiramphidae species in the Indo-Australian region are restricted to freshwater (Greenfield and Thomerson 1997).

The distributional range of *H. r. hildebrandi* extends along the Caribbean coast of Central America from Mexico to the Gulf of Uraba in Colombia (Collette 2004, Miller et al. 2005). The sub-species is considered marine and estuarine, commonly found in mangrove forests (Greenfield and Thomerson 1997), and coastal lagoons (Schmitter-Soto 1998, Díaz-Ruiz et al. 2003, Collette 2004). For example, they have been collected in the Laguna de Bacalar in southern Mexico (Schmitter-Soto 1998) and the Tortuguero National Park in Costa Rica (Winemiller and Leslie 1992).

Previous specimens collected in Honduras have been from estuarine and marine systems or from freshwater systems with a direct connection to brackish or marine water (see NeoDat, <http://www.neodat.org>). Here, we report the first record of *H. r. hildebrandi* in Honduran freshwater (see Reis et al. 2003) as well as in a landlocked freshwater body of water.

MATERIALS AND METHODS

In January 2003, three specimens of *H. r. hildebrandi* were collected by personnel from the Honduras Center of Studies of Contaminants Control (CESCCO) along the shore of the Francisco Morazán El Cajón ("El Cajón") reservoir. El Cajón is located in northeastern Honduras (Figure 1) at 15°04'N, 87°33'W (Central Offices), at an

altitude of 285 m above sea level, between the municipalities of Santa Cruz de Yojoa in the department of Cortés, Victoria in the department of Yoro, and Lagos, La Libertad, Minas de Oro y Mcámbar in the department of Comayagua. The reservoir spans an area of 94 km² with a perimeter of 469.7 km, and a maximum depth of 185 m.

Specimens were collected as part of a field assessment following a fish-kill and were dead upon collection. Specimens were immediately fixed in 10% formalin, rinsed in tap water, and then transferred to 70% ethanol for preservation. Standard length (SL, mm) was measured using digital calipers and specimens were weighed (wet weight, g). Fish were identified based on standard characters (Greenfield and Thomerson 1997) and deposited in The University of Southern Mississippi Museum of Ichthyology (voucher number: USM 31216).

To determine the presence of the sub-species in other Central America freshwater bodies of water, we queried NeoDat (<http://www.neodat.org>), an internet database specializing in collections of neotropical fishes.

RESULTS

Three specimens of *H. r. hildebrandi* were collected and identified based on the following combination of characteristics (Greenfield and Thomerson 1997): lower jaw much longer than rest of head but shorter than half of the standard length; scales absent or only a few present on anterior part of the dorsal and anal fins, total gill rakers on first arch more than 38; dorsal plus anal rays usually total more than 30. Specimen identification was confirmed by B. Collette (Collette pers. comm., National Marine Fisheries Service Systematics Laboratory, Washington, DC, USA). Standard length and wet weight of fish were 124.4, 122.5, and 116.7 mm; and 7.6, 6.8, and 5.4 g, respectively.

Results from the database queries conducted showed that *H. r. hildebrandi* has been collected in Mexico, Belize, Guatemala, Honduras, Costa Rica, and Panama. Most of these collections came from coastal ecosystems. Unreported collections of *H. r. hildebrandi* from fresh-

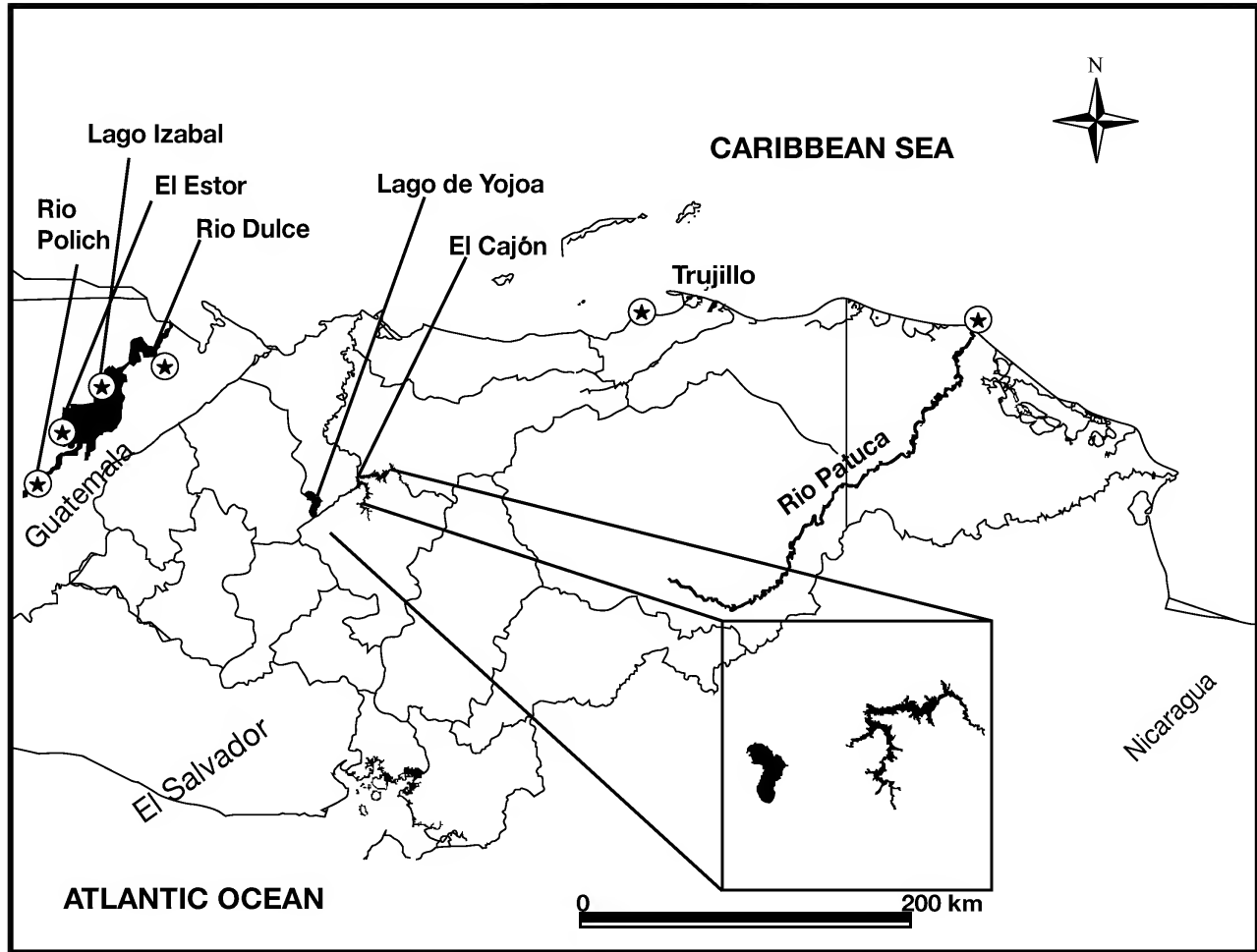


Figure 1. Map of Honduras showing the location of the hydroelectrical dam “El Cajón” and Lake Yojoa. Circled stars depict locations of previous unreported collections of *H. r. hildebrandi* in Honduras and Guatemala.

water systems that have direct connections to brackish waters including the following localities in Guatemala: Lake Izabal (USNM-114261, USNM-134705), Río Dulce (UMMZ-197188), Río Polochic (AMNH-35043, CAS-45429), and El Estor (USNM-134706). An additional site was located in the Río Patuca (UMMZ-199576) in Honduras and a site in Honduras located 30 km east of Trujillo (B. Collette, pers. comm., see Figure 1).

DISCUSSION

In Central America, Honduras is quite possibly the country with the least studied ichthyofauna. The need for systematic studies of Honduras freshwater fishes has been clearly recognized (Carr and Giovannoli 1950, Miller 1966). Recently, Lyons (2005) who focused on a disjunct distribution of the genus *Sicydium* in Mexico and Central America emphasized the need for a stronger knowledge base of the ichthyofauna in Honduras. Accordingly, it

would not be surprising to discover range expansions of fishes in Honduras or other regions where ichthyological research is scarce. The novelty, however, is to encounter in an inland freshwater body a species from a family of fishes that is thought to primarily exist in coastal and marine waters.

Museum records demonstrate the presence of *H. r. hildebrandi* in coastal lagoons and marine environments of Honduras, as well as freshwater in Guatemala. Specimens collected in Lake Izabal and along river systems in the region, document the presence of the species in Guatemalan freshwater systems with connections to brackish water (Miller 1966). Yet, our report documents the first record of *H. r. hildebrandi* from an inland, landlocked, freshwater system, indicating the species may be established and recruiting in freshwater. It is unknown at what point *H. r. hildebrandi* may have been established in El Cajón, since the reservoir was constructed in 1985,

and no data exist in relation to the status of ichthyofauna diversity both before and after the dam was built.

Lake Yojoa, another freshwater body near El Cajón, was surveyed by Martin (1972) and Cruz (1985), but the presence of *H. r. hildebrandi* was not reported in their surveys. Currently this species is common in the littoral zone of the lake (W. Matamoros, pers. obs.), and we infer that the arrival of *H. r. hildebrandi* in the area happened after 1985. However, the means of dispersion employed by the species *H. r. hildebrandi* to expand its range is unknown.

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USE OF *DIADEMA ANTILLARUM* SPINES BY JUVENILE FISH AND MYSID SHRIMP

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INTRODUCTION

The long-spined sea urchin (*Diadema antillarum* Phillipi) is an important element in the structure and function of coral reef communities. Regarded as a key herbivore in reef communities, grazing by *D. antillarum* shifts community dominance from macroalgal cover to live coral (Lessios 2005, Tuya et al. 2004). *Diadema antillarum* is primarily found in shallow coral reef and seagrass environments but can reside in a wide variety of habitats (Lessios 1998). This animal generally remains in sheltered areas during the day and moves to grazing sites during the evening. Its activities can create grazing halos around reefs (Ogden et al. 1973). Additionally, urchins represent potential biogenic structure and refugia for fish and invertebrates.

The availability of shelter influences the survivorship and recruitment of juvenile reef fishes (Shulman 1985). Structurally complex habitats allow prey to escape predation as they utilize small spaces for refuge (Caley and St. John 1996). Literature suggests that the urchin spines represent a complex three-dimensional structure in which small fish can evade predators. Consequently, the utilization of urchin spines as a structural habitat has been shown to increase survival of juvenile fish (Hartney and Grorud 2002). Studies have also noted that swarms of mysid shrimp (*Mysidium* sp.) associate with *D. antillarum* as a source of protection against fish predation (Twining et al. 2000). Additionally, urchin size may affect how frequently fish use this complex biogenic habitat (Hartney and Grorud 2002). Some fish have been shown to associate with urchins which possess spines that are proportionate to fish body size (Lissner 1978), and *D. antillarum* have the unique ability to regulate body size in response to resource availability (Levitan 1988, 1989). Therefore, exploration of how urchin test size correlates with the presence of juvenile fish and invertebrates may be important for assessing the urchin-fish/invertebrate relationship.

This research has the following objectives: 1) identify the size structure of *D. antillarum* among 3 coastal bays of St. John, United States Virgin Islands and 2) determine

relationships between urchin presence and spine utilization by fish and mysid shrimp.

Study Site

Field studies were conducted at 3 coastal bays in St. John, United States Virgin Islands including: Hurricane Hole, a fringing mangrove and seagrass community; Greater Lameshur Bay, a predominantly hard substrate-coral reef community; and Little Lameshur Bay, a hard substrate-coral reef community interspersed with seagrass and unvegetated habitats.

METHODS

To assess how *D. antillarum* size influenced fish and invertebrate presence, urchins were counted and measured and associated mysids and fish were recorded in 2 surveys. First, 410 *D. antillarum* were counted and test diameter was measured and classified into size categories (0–30 mm, 30–60 mm, 60–70 mm, 90–20 mm, 120–150 mm, > 150 mm). Data were recorded in the field, and all measurements were taken on individual days at each site to eliminate the possibility of measuring the same urchin twice. Urchin size-frequency data were analyzed using a non-parametric Kruskal Wallis Rank Analysis to determine whether urchin size differences existed among sites. When present, samples of fish were collected using a slurp gun, then enumerated and identified to species. An additional 628 urchins were surveyed in Little Lameshur Bay to determine the utilization of *D. antillarum* spines by mysids and fish. Fish and mysid presence was then tabulated to propose utilization of spines as refuge/biogenic habitat. In some cases, surveys did not identify certain fish species during sampling *a priori*, therefore they were not included within tabulated results.

RESULTS AND DISCUSSION

The *D. antillarum* size-frequency distributions found in Greater Lameshur and Hurricane Hole indicate a relatively normal size distribution, with a modal test diameter

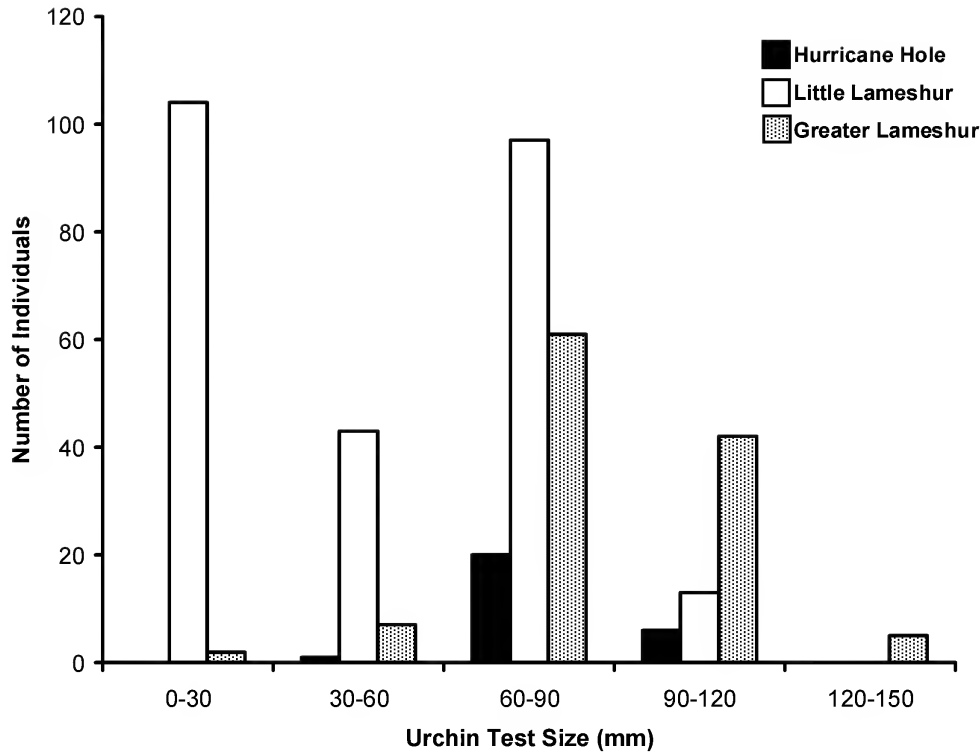


Figure 1. *Diadema antillarum* size frequency distribution. Bars represent total number of urchins within each test diameter size class (mm) at each of the 3 study sites.

within the 60–90 mm size class (Figure 1). The Little Lameshur site differed, however, with a mode at 0–30 mm, which may reflect the presence of recently recruited juveniles and a different year class present in the samples. This disparity resulted in a significant difference in mean test size ($H = 151$, $P < 0.001$) between Greater Lameshur (sample mean = 85.5 mm) and Hurricane Hole (80.5 mm) compared to Little Lameshur (47.2 mm). Additionally, the largest size classes of urchins occurred only at Greater Lameshur (Figure 1).

Our exploration of the *Mysidium* sp. and *D. antillarum* association suggests that urchin test diameter influences mysid presence. Whereas swarms occurred over groups of smaller urchins, they were only observed over individual urchins in the 90–120 mm size class. *Mysidium* sp. swarms were found over urchins at all sites, with fre-

quencies of occurrence of 3.8% at Hurricane Hole, 6.8% at Greater Lameshur, and 2.8% at Little Lameshur (Table 1). *Mysidium* sp. is known to occur in swarms just off the bottom of the sea floor near structurally complex, three-dimensional substrata, including *D. antillarum* (Hahn and Itzkowitz 1986). In a previous study on the homing behavior of *M. gracile*, it was found that mysids swarm at given sites during the day and disperse during the night. It was suggested that mysid shrimp use some type of homing behavior to re-coalesce into discrete schools after nocturnal dispersal (Twining et al. 2000).

The most abundant fish associated with sea urchin spines was *Haemulon flavolineatum* (French grunt). This species was only collected from urchins of a test size > 60–90 mm and only in Little Lameshur Bay (Table 1). This does not mean that they were not present in the other

Table 1

Mysid shrimp and fish utilization of *Diadema antillarum* spines. (NA = not assessed during specific site survey).

Sites	<i>Diadema antillarum</i> (N)	<i>Mysidium</i> sp. Schools	<i>Haemulon flavolineatum</i> Schools (mean#/school)	<i>Canthigaster rostrata</i>	<i>Pareques acuminatus</i>
Hurricane Hole	26	1	0	0	0
Greater Lameshur	117	8	0	NA	0
Little Lameshur East	628	17	NA	10	0
Little Lameshur West	259	8	9 (11.2)	NA	1

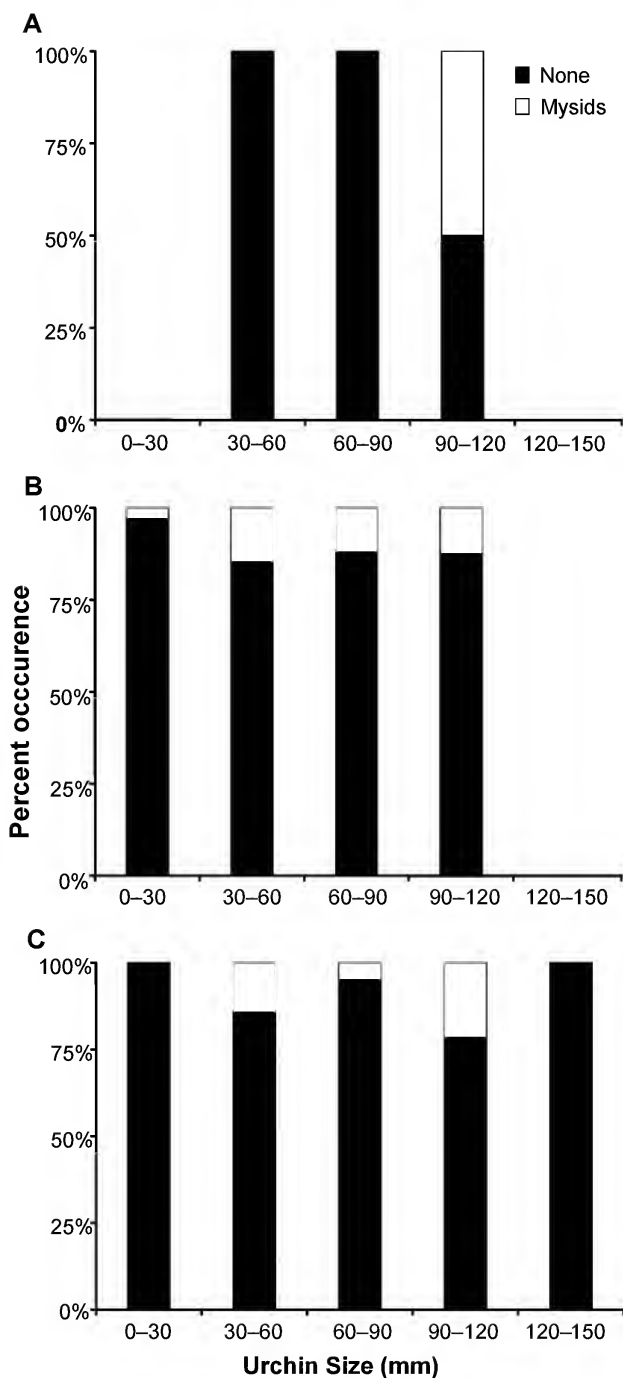


Figure 2. *Mysidium* sp. utilization of *Diadema antillarum* spines. Bars represent percent frequency of occurrence of mysids among spines of urchins in each size class. A) Hurricane Hole. B) Little Lameshur. C) Greater Lameshur.

bays, but rather that our survey did not identify utilization of *D. antillarum* in these bays. McFarland and Kotchian (1982) showed that *H. flavolineatum* commonly forms mixed schools with mysid shrimp (genus *Mysidium*). The schooling behavior of these different organisms into large complexes may relate to the morphological similarities that grunts have with mysid shrimp. The postulated benefits for the fish include protection (at smaller sizes) and use of mysids as food (at larger sizes).

In addition to *H. flavolineatum*, we observed 2 other species that have not been previously recorded from *D. antillarum* spines. We observed and collected *Canthigaster rostrata* (sharpnose puffer) from within the spines of urchins in Little Lameshur Bay (Table 1). The puffers were observed and collected deep within the spines of urchin groups comprised of 3–6 individuals (observation Bologna and Townsend). Previous studies of *C. rostrata* in St. Thomas, USVI indicate that this species is significantly more abundant where predators are more abundant, in comparison to other prey species (Shulman 1985). Sharpnose puffers are toxic and may survive in predator rich areas because they are not potential prey for piscivores (Hixon and Beets 1993). *Canthigaster rostrata* is, however, preyed upon by some bony fish, including *Sphyrna barracuda* (Randal 1967), which was frequently observed in Little Lameshur Bay (Bologna observation). Therefore, it is possible that juvenile sharpnose puffers utilize urchin spines as refuge from predators, enabling this species to co-exist in these reef communities. A *Pareques acuminatus* (high-hat) was also observed and collected from deep within the spines of *D. antillarum*. This fish was very cryptic, and its body form and pigmentation resembled urchin spines. Although we only collected one *P. acuminatus*, we believe that its presence and its cryptic appearance among the urchin spines may suggest Batesian mimicry between *P. acuminatus* and *D. antillarum*.

Through our research, we were able to identify 3 types of juvenile fish within urchin spines, as well as determine that urchin test size plays a role in juvenile fish/mysid shrimp utilization. Future investigations of the association between *H. flavolineatum*, *C. rostrata*, and *D. antillarum* are necessary to understand the relationship between these juvenile fish and urchins. Additionally, further studies with *P. acuminatus* need to be pursued in order to determine whether our observation was a random occurrence or if this species uses crypsis and mimicry of urchin spines as a predation refuge during early juvenile stages.

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COLOR VARIATION IN THE CARIBBEAN CRAB *PLATYPODIELLA SPEC-TABILIS* (HERBST, 1794) (DECAPODA, BRACHYURA, XANTHIDAE)

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INTRODUCTION

Platypodiella spectabilis (Herbst, 1794) is a relatively small crab (about 10 mm carapace width) found in or near coral reefs and rocky shorelines throughout most of the Caribbean and tropical western Atlantic. Records are known from as far north as Bermuda (Chace et al. 1986, in Sterrer 1986, as *Platypodia spectabilis*) and as far south as Rio de Janeiro, Brazil, including the Fernando de Noronha Archipelago and Trinidad Island (Melo 1998: 490) and the state of São Paulo (Coelho and Ramos 1972, Fransozo et al. 2001). Thus, the range of the species is some 7,000 km from northern to southern extent. Distributional records within this range, and extending westward into the Gulf of Mexico, can be found in Rathbun (1930), Felder (1973), Powers (1977), and Abele and Kim (1986). Because of its spectacular coloration and color pattern, *P. spectabilis* is often depicted in faunistic guide books (e.g., Humann 1992, Humann and DeLoach 2002), and the species is sometimes referred to as the calico crab (e.g., Chace et al. 1986) or gaudy clown crab (Williams et al. 1989, McLaughlin et al. 2005).

The use of color in brachyuran crab systematics, and in particular the use of subtle color differences to suggest or differentiate cryptic or morphologically similar species, is now well documented (e.g., see Campbell and Mahon 1974 for species of *Leptograpsus*, Williams and Felder 1989 for species of *Menippe*, Zimmerman and Felder 1991 for species of *Sesarma*). Less clearly understood is why color patterns and intensities can sometimes vary appreciably within a species, even within narrowly restricted geographic regions. An appreciation of color patterns is critical to correctly identifying species for conservation and resource management purposes, yet often color patterns and ranges are unreported, causing confusion and sometimes misidentifications. Here we document a wide range of color patterns in a small Caribbean xanthid crab based on specimens collected in essentially the same habitat at the same time of year.

MATERIALS AND METHODS

As part of a biodiversity survey of Caribbean crypto-faunal invertebrates, we sampled several habitats from shallow waters off Guana Island, British Virgin Islands, during the summers (June–August) of 1999–2002. Specimens of *P. spectabilis* collected during that survey came almost exclusively from an area of a few square meters at our North Bay collecting site, where they were found in interstices of dead coral (mostly clumps of dead *Porites*) in shallow water (≤ 1 m) (Station 65 of the Zimmerman/Martin survey of Guana Island in 2000 and 2001). Collections were made by crushing clumps of dead coral and removing by hand the invertebrates they contained. In this manner, a large number of specimens of *P. spectabilis* were collected (including all of the photographed specimens except Figure 2d), especially in the year 2001.

Similarly-sized crabs were photographed while alive or just after immersion in ice water, a technique that rapidly kills tropical crabs while preserving their color for up to 12 hr. Photography was done by T.L. Zimmerman (Figures 1a–f; Figure 2a–c) and Leslie Harris (Figure 2d). Associated field voucher numbers are listed in the figure captions.

After being photographed, crabs were preserved in either 70% or 95% ethanol for eventual transfer to and storage in the Crustacea collections at the Natural History Museum of Los Angeles County. One ovigerous female from the North Bay site (photographic voucher number Vc0-796, Figure 1b), with a carapace width 10.5 mm and carapace length 7.1 mm, was the parental female that formed the basis of the first description of larvae in this genus (Fransozo et al. 2001).

RESULTS

As is evident from the accompanying figures (Figures 1 and 2), specimens of *Platypodiella spectabilis* collected in the British Virgin Islands (and presumably elsewhere) exhibit a wide range of color patterns. The background color varies from a light cream or beige (Figure 1a–d) to an intense yellow (Figures 1e, f; 2a–c). Regularly-spaced and nearly circular black spots ringed with white may be present on the carapace (Figure 1c, e), or the carapace can

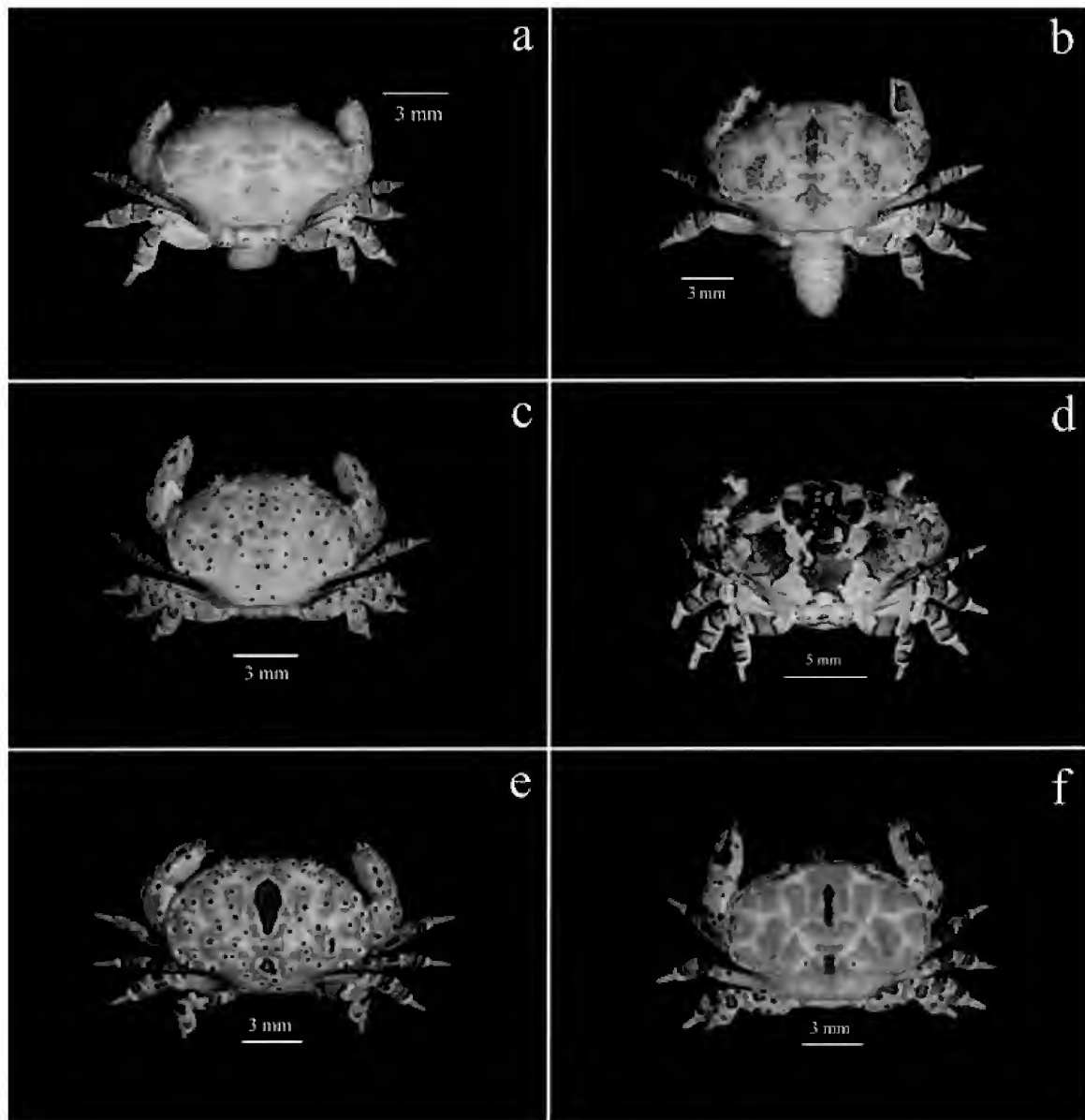


Figure 1. Color variation in the xanthid crab *Platypodiella spectabilis* (Herbst, 1794). a: muted background yellow, no spots, no brown patches (female, Vc0-799); b: muted background yellow with many muted large brown patches (female, Vc0-796); c: muted background yellow with spots, no brown patches (male, Vc0-800); d: muted background yellow with intense large brown patches, no spots (male, Vc0-792); e: intense background yellow with few small brown patches with spots (male, Vc0-798); f: intense background with few small brown patches, no spots (male, Vc0-801). All photographs by T. Zimmerman.

lack any semblance of similar-sized spots (Figures 1a; 2b). Irregularly-shaped brown patches sometimes occur on the carapace, and are often found on the cardiac and gastric regions (Figures 1d; 2a–c); in some specimens (e.g., Figure 2c) the brown patches are coalesced to form the majority of the color on the dorsal carapace, with only limited areas displaying white or yellow. Some individuals exhibited both irregular brown patches and more regularly-spaced and evenly-sized spots (Figure 1e). Pereiopods typically bear yellow, white and brown patches so as to appear banded. Usually the order of color on a given pereopodal

article is, from the proximal to distal end, yellow followed by brown followed by white, such that the distal end of the article is white or light beige (e.g., Figures 1a, b, d; 2b). However, in some specimens the segments of the legs are almost completely brown (Figure 2c), and in others the yellow area is bordered on both sides (rather than only on the distal side) by brown (Figure 1d).

Sex of the crab does not appear to have any noticeable effect on the color pattern; figures include both males (Figures 1c–f; 2a–b) and females (all others except Figure 2d, a juvenile). The juvenile we collected was lighter

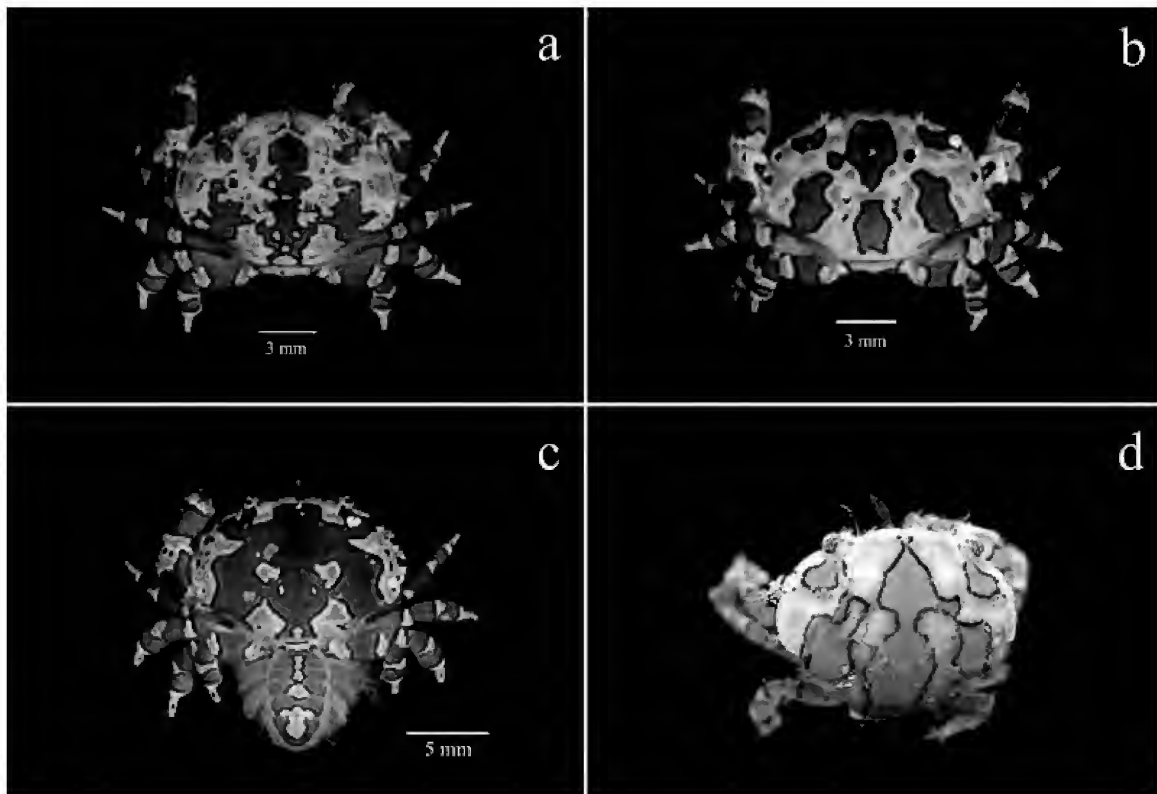


Figure 2. Color variation in the xanthid crab *Platypodiella spectabilis* (Herbst, 1794), continued. a: coalescent solid brown patches with some muted regions (and possibly spots) over diffuse intense yellow background (male, Vc0-797); b: distinct brown patches with distinct patches of intense yellow background color (male, Vc0-794); c: coalescent solid brown patches over diffuse intense yellow background (female, Vc0-793); d: coloration pattern in a juvenile (H-2037) before carapace regions are clearly demarcated. Photographs a–c by T. Zimmerman; d by Leslie Harris.

overall, with a background carapace coloration that was off-white and with a more orange (less brown) color pattern dorsally (Figure 2d).

DISCUSSION

Color plays an important role in species identification and presumably in species-species recognition among decapods. Additionally, knowledge of coloration and color variability can assist in the recognition of species by conservationists and resource managers without extensive taxonomic training. Coral-associated crabs are among the most colorful of all decapods, with trapeziids and tetraliids well known in this regard; coral-associated carpilliids and eriphiids are also often very colorful. However, few crab species exhibit coloration as striking as in *P. spectabilis*, and there are few reports of colors or color patterns that vary to the extent shown here within a known species and within a very small geographic range (in our case, within meters). A similar situation exists for a tropical hermit crab, *Calcinus gaimardi*, in the western Pacific with at least 2 distinct color morphs that occur sympatrically (C. Tudge, pers. comm., Morgan 1991, Tudge 1995).

Although it was stated earlier that the wide range of color patterns in this species might indicate a formerly unrecognized species complex (Frasozo et al. 2001), there is virtually no doubt that all specimens illustrated here belong to the same species. Even at the larval level, the widespread *P. spectabilis* does not appear to vary much across its rather large range. Frasnoso et al. (2001) documented slight differences in the morphology of reared larvae of this species from the Caribbean and from Brazil, but overall, despite the geographic distance separating the parental females, larvae from the 2 areas were found to be quite similar.

The genus *Platypodiella* was erected by Guinot (Guinot 1967: 562) to accommodate 4 species formerly treated as *Platypodia*. Two of the species, *P. gemmata* (Rathbun, 1902) and *P. rotundata* (Stimpson, 1860) are known from the eastern Pacific. Garth (1991: 131), in discussing the Galapagos crab fauna, pointed out that the 2 Pacific species are possibly the adult (described as *P. rotundata*) and the juvenile (*P. gemmata*) of the same species, with the name *P. rotundata* having precedence. The other 2 species are Atlantic, with *P. picta* (A. Milne Edwards, 1869) restricted to the eastern Atlantic and *P. spectabilis* (Herbst,

1794) known from the western Atlantic. Guinot (1967) remarked on the similarities between species of this genus and those of *Platyactaea* and, to a lesser extent, to species of *Atergatis* and *Atergatisopsis*, as well as to members of *Platypodia*. The latter 3 genera are sometimes considered members of the xanthid subfamily Zosiminae (e.g., see Serène 1984, Clark and Ng 1998). It would be interesting to examine the range of color patterns exhibited by species in these supposedly related genera to see if color variability has a phylogenetic component.

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